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STATEMENT OF OWNERSHIP AND MANAGEMENT

Male Mate-Locating Behavior in the Desert Hackberry Butterfly, *Asterocampa leilia* (Nymphalidae)

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Abstract. The mating system of the desert hackberry butterfly, *Astero-campa leilia*, is described with special reference to the site tenacious mate-locating behavior of the males. Males occupy perches on or next to the larval foodplant, desert hackberry (*Celtis pallida*). Other males are not tolerated within several meters of a male's perch site and are chased away when they fly nearby. Males occupy perch sites in the morning. Some hackberry trees are more likely to be used as perch sites than others and males at these sites experience the highest rate of contacts with females and other males. Females passing a perch site are chased, courted, and, if receptive, mated. The data indicate that males defend perch sites as a means of maximizing potential contacts with newly-emerged, virgin females leaving the plant adjacent to their perch site.

Introduction

Male butterflies show a wide interspecific diversity in the extent to which they are site tenacious in their mate-locating behavior (Scott, 1974, 1975, 1982). At one extreme males are not tied to any given site but fly widely through the environment searching for females. This strategy has classically been referred to as patrolling. At the other extreme males are very site tenacious and an individual may defend a space on a hilltop or other place for several days usually during some restricted daily activity period (Powell, 1968; Baker, 1972; Douwes, 1975; Suzuki, 1976; Davies, 1978; Bitzer & Shaw, 1979, 1983; Callaghan, 1982; Lederhouse, 1982; Alcock, 1983, 1985; Wickman & Wiklund, 1983; Knapton, 1985; Wickman, 1985; Alcock & O'Neill, 1986). In territorial species males interact with other males in ways that are very different from their interactions with females. Aerial combat occurs in the form of ascending flights and wing contact. Between these extremes of patrolling and highly territorial species there are species in which males, although showing some site tenacity,

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may only briefly occupy a site and be less aggressive toward conspecifics. Detailed studies of these behaviors are lacking.

Males of the desert hackberry butterfly (*Asterocampa leilia* Edwards) occupy perch sites near the larval foodplant, desert hackberry (*Celtis pallida* Torrey), that they appear to defend against conspecific males (Austin, 1977). Our preliminary observations of this species in central Arizona suggested that individual males do not spend much time on specific sites. Here we describe in detail the perching behavior of the males of this species and document the extent to which males are site tenacious and their perch site preferences. The discussion focuses on the ecological circumstances favoring this sort of mate-locating behavior, especially in comparison with mate-locating techniques in other species.

METHODS

Asterocampa leilia males and females were observed and collected at two flat or gently sloping sites near water courses in the upper Sonoran desert habitat typical of central Arizona. Our primary site was near the Salt River about 40 km northeast of Tempe, Arizona, and the other site, used primarily for observations of courtship with hand-reared females, was along Sycamore Creek about 70 km from Tempe. At both sites the large vegetation included paloverde (*Cercidium* spp.), mesquite (*Prosopsis* spp.), saguaro cactus (*Carnegia giganteus* (Engelmann) Britton and Rose) and desert hackberry (*Celtis pallida*).

At the Salt River site we identified a triangular, 1700 m^2 area that extended on the north to the beginning of a small mountain range, on the south to a line of paloverde trees, on the west to a low ridge extending out from the mountains, and on the east to a small dry wash. This area contained fifteen discrete clumps of hackberry that varied in size. Males were captured and carefully marked by writing numbers on the dorsal and ventral hindwings with a felt-tipped marking pen (Sanford Sharpie[R]).

On 17 mornings from 6 May to 11 June in 1985 we walked through the study area at 30 min intervals and noted the location and identity, if marked, of each male seen perched. We also observed the activities of males at individual perch sites, especially those that were most often occupied, and recorded the interactions between the perch site occupant and intruding individuals of both sexes. Wherever possible these observations were made on marked males that occupied perch sites.

Courtship, Copulation, and Spermatophore Counts

Successful courtships and the ensuing copulations were elicited by releasing hand-reared virgin females near perched males in the field. The females were reared from eggs collected by placing field-caught females in cages with a sprig of the larval foodplant.

After copulation, mated pairs were killed and stored by freezing. Later the females were thawed, weighed, and dissected under insect Ringer's solution. The bursa copulatrix of each female with its contents was examined and weighed to the nearest 0.01 mg. The male of each pair was also thawed and weighed.

To estimate the frequency with which females mate, we collected and froze a sample of females from the population. They were later thawed and dissected under insect Ringer's solution, and the contents of the bursa copulatrix of each was examined. The wing wear of these females was assessed as an indicator of age. Each female was placed in one of three wing wear categories: fresh — little or no scale loss or tattering, worn — substantial scale loss or tattering on one or two wings, and very worn — substantial scale loss or tattering on all wings.

Statistical Summary and Tests

Parametric summary statistics are given as the mean ± the standard deviation. The results of all statistical tests were evaluated at the 0.05 level of significance.

RESULTS

Spatial Organization and Daily Pattern of Male Activity

Male perch sites were found in only 20 locations within the Salt River study area. A perch site was an area of approximately 1-2 m^2 in all cases except one on or immediately adjacent to a hackberry tree, confirming Austin's (1977) result. Some sites were occupied more frequently than others. In 97 censuses made over 17 days the average occupation frequency among the 20 perch sites was 21.9 ± 20.6%; however, the two most frequently occupied sites were occupied in 83.5% and 61.9% of the censuses, respectively. Only one of the hackberry clumps in the study area never had a male perched next to it.

The behavior of the males followed a daily pattern. Males occupied perch sites when they first became active in the morning. Fig. 1 shows the number of males seen perching as a function of the time before and after the observed time of peak activity. Peak activity was defined as the time at which the number of sites occupied reached the maximum number observed on a given day. The average time of peak activity was 900 MST (range: 800-1000). Late in the morning the males moved into the shade of hackberry trees and became inactive.

Site Tenacity of Males

One-hundred and two males were captured, marked, and released. Of these 34% were resighted at some point after release (Fig. 2). After being marked and released, a male typically left the area and was not seen again on that day. The probability that a marked male would be resighted was highest the day after marking (18%). The longest time between release and the last resighting of a male was 10 days.

A male did not occupy a given perch site for long. Fig. 3 shows the distribution of site occupation durations observed on single days during the study. Most males were on a site for only 30 min or less on any given day. However, one male was observed on the most frequently occupied
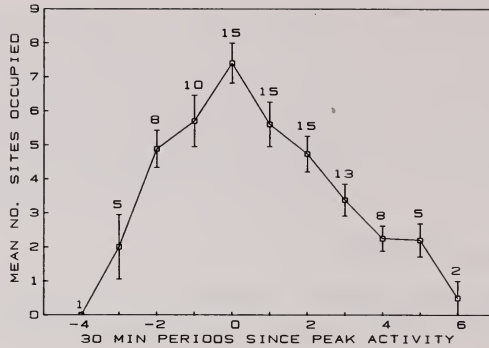
Fig. 1.   The daily pattern of perching activity for A. *leilia* males averaged over 17 days. The number above each indicates the sample size.
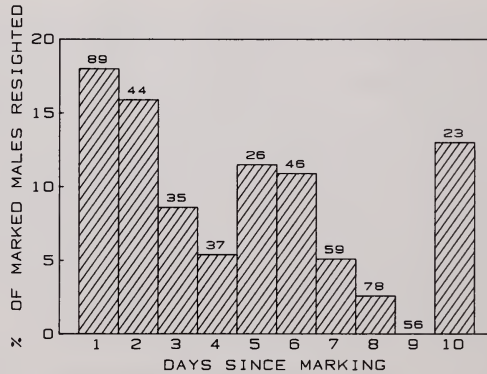
Fig. 2.   The probability of resighting previously marked males as a function of the days since they were marked. The number above each bar is the number of males in the population marked on day zero that were available on a given day for recapture.
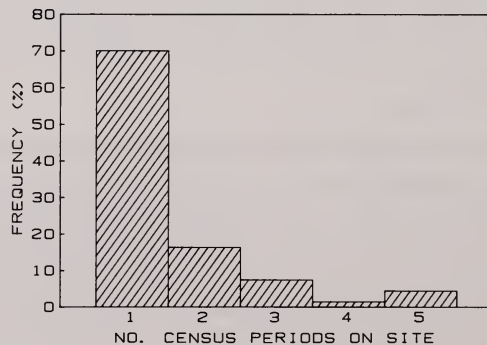
Fig. 3.   For all sites that were seen occupied by a marked male this figure shows the duration of site occupation as the number of consecutive census periods on the same day that the male was seen on a given site (n = 67).

site on the study area for 5 census periods one day and then two more on the next. It is possible our censusing activities scared males prematurely from their perch sites; some males did take to wing when we approached but they returned to their perch after a brief flight. In any event we took some pains not to disturb males during the censuses.

Site Defense

Males perched on sand, rocks, and low vegetation (especially the hackberry tree) (Fig. 4). From these positions a male flew out and chased passing conspecifics, heterospecific butterflies, other insects (flies, wasps, etc.), birds, and even thrown stones. Conspecific males flying near a male's perch were typically approached and chased on the wing for several meters. In this species, no male-male interactions led to ascending flights. Occasionally a male perched near the resident without being detected. Such intruders were not detected until they flew, at which point they were approached and chased from the area. In 73% of 37 male-male interactions involving at least one marked male, the male that was originally perched in the area returned alone and reoccupied the site. This is significantly more frequently than expected from chance ($\chi^2 = 7.81$, 1 df, $p < 0.05$).

On occasion a male spontaneously flew up from his perch and patrolled an area by flying back and forth in front of the hackberry tree for a few seconds before perching again. When the resident alit after such a patrol flight or after an interaction he typically perched on or within a meter of his original perch.

The behavior of the males varied with the site and with the time of the morning. The more attractive sites were more likely to be occupied for more than one period by a single male (Table 1; $\chi^2 = 11.5$, 1 dr, $p < 0.05$). Males that occupied the two most popular sites tended to stay on them throughout the activity period in spite of frequent intrusions by other males. Eighteen perched intruders were observed at these sites in 528 min of observations during the hour surrounding the time of peak

Table 1.   How site identity affects the number of consecutive census periods that the site will be occupied by the same male. Sites 1N and 15 were the most frequently occupied sites.

No. of periods occupied	Sites 1N and 15	All other sites
1	39%	82%
2-3	39%	18%
4-5	22%	0%
Total observations	18	49

Fig. 4.   Males of *A. leilia* perched on their sites. A male perched on staghorn cholla (above) and on the ground (below).

activity, while no perched intruders were observed in 107 min of observations on other sites at the same time.

Males do spontaneously abandon sites. Some sites were less likely to be abandoned for no apparent reason than less attractive sites. For example, during a total of 803 min of observation at sites 15 and 1N only one abandonment was observed. In contrast 6 abandonments were observed in 111 minutes of observations at three other sites (1S, 3S, and 3N) during the same time period. There were significantly fewer abandonments at site 15 and 1N than expected from the time spent observing there $\chi^2 = 35.5$, 1 df, p < 0.05).

Competition for sites is intense as indicated by the fact that when we sequentially removed 10 males during one hour from the most frequently occupied site, the site was reoccupied within a few minutes by a new male after each removal. Furthermore, the intensity of the competition changed over the morning. This was evident in two ways. First, if a male observed on a site in one census was not there when the site was censused 30 min later, at the time of peak activity there was a greater than 50% chance that the site would be occupied by a new male (Fig. 5). Late in the morning sites were rarely reoccupied if for some reason the male left. Second, the frequency of perched intruders waned as the morning progressed (Fig. 6; Spearman rank correlation coefficient = −0.87, p < 0.05).

Courtship and Copulation

The rate of appearance of wild females varied among sites. Females appeared at a rate of 0.0177 per min (790 min of observation) and 0.0123 per min at (163 min of observation) at the first and second most frequently occupied sites, respectively. In contrast, during a total of 203 min of observation no females were seen at several other sites when a male was present.

A total of 6 successful and 8 unsuccessful courtships were observed during this study. All successful courtships involved hand-reared virgin females released near males. On three occasions during observations of males on sites the male chased a female and did not return; the pair flew off so quickly we were unable to determine the outcome of the interaction.

When a female flew by a perched male he immediately took wing and followed the female. In successful courtships the female immediately perched in vegetation near the male's perch site. The male then landed behind the female, moved up beside her, and began attempting to insert his abdomen between the female's hindwings. The female then either remained still and permitted the male to couple or moved away from the male for some time before becoming still and permitting copulation. In unsuccessful courtship the female did not perch when the male approached and in 5 cases engaged in ascending flights with the male in pursuit. The male abandoned the female and returned to his perch after an ascending flight interaction.
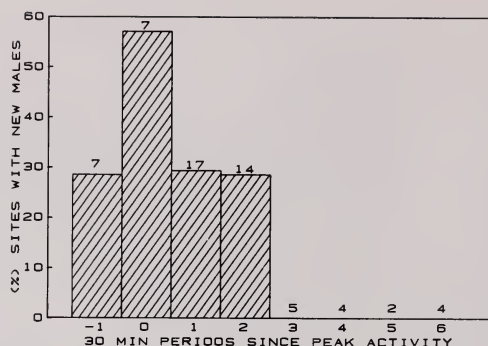
Fig. 5.   The likelihood that a previously occupied site will be occupied by a new male in the census period after the site was seen to be occupied is plotted against the time of the post-occupation census. The sample size for each time period is shown above each bar.
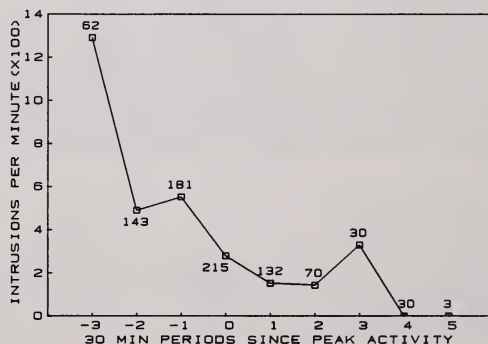
Fig. 6.   The rate of appearance of undetected perched intruders is shown as a function of the time since peak activity. The number of minutes of observation from which the data point was calculated is shown above each point.

Copulation averaged 49 ± 16.8 min (n = 6, range: $21 - 65$ min). During copulation a male formed a spermatophore and deposited some loose white secretions within the female's bursa copulatrix. The mass of material averaged 2.49 ± 0.78 mg (n = 7, range: $1.47 - 3.73$ mg) which correspond to $2.96\% \pm 0.59\%$ (n = 7, range: $1.9 - 3.71\%$) of the male's estimated precopulatory body weight. The quantity of material passed was significantly positively correlated with the estimate of a male's precopulatory body weight (r = 0.797, t = 2.96, 5 df, p < 0.05).

Twenty-six females were collected in the field and the contents of the bursa copulatrix of each was examined. In this sample 73% were fresh, 19% worn, and 7% very worn. No female carried more than one spermatophore and three (all fresh) had bursae that were empty.

DISCUSSION
Characteristics of Male Perching Behavior

The data reveal several features of the perching behavior of *A. leilia*. First, as Austin (1977) suggested, males perch most often near *C. pallida* trees. Second, a perched male does not tolerate other males in their perching area but are not likely to defend any given perch site for long. Third, males occupy and defend perch sites for only a restricted part of the day. Males became inactive toward the middle of the day and roosted well within *C. pallida* trees on or near their site. Such temporal restrictions on site-tenacious strategies of mate-location are common in butterflies (Callaghan, 1982; Alcock, 1983; Wickman, 1985) and are probably best explained by heat stress due to high midday temperatures (Rawlins, 1980; Kingsolver and Watt, 1983) which favors abandonment of perches in the late morning or by variation during the day in the availability of receptive females. Fourth, some sites are strongly preferred over others as indicated by the frequency with which they were occupied, the rate at which undetected intruders perched on them, and the rate with which they were abandoned by males. Similar preferences are found in other perching species (e.g. Bitzer & Shaw, 1979; Lederhouse, 1982; Alcock, 1983). Finally, the sites that were preferred by males were also those visited most frequently by females although it is not clear that these females were receptive. This has been shown for three other territorial species of butterflies (Davies, 1978; Lederhouse, 1982; Wickman, 1985).

The Function of Male Perch Site Placement and Defense

We interpret site occupation and defense as a mate-locating tactic in this butterfly. The sites contained no nectar or water resources that might be of interest to males or females and so defense of resources for personal use or to gain access to females seems improbable. Why then are the sites on or next to the larval foodplant? There are at least two possible hypotheses. A male may perch near the larval foodplant to gain access to females that come to oviposit. Such behavior has been observed in bees, dungflies, odonates, and many other insects (Thornhill & Alcock, 1983). However, there are apparently no benefits from trying to intercept mated females in that *A. leilia* females mate only once.

We conclude that males perch near the larval foodplant to maximize their chances of contacting virgin females as they emerge on their first flight. However, this assumes that the larvae pupate on the larval foodplant. This is likely. We have found cast pupal skins on *C. pallida*, and the pupae bear a striking resemblance to the leaves of the host plant, suggesting that the larvae routinely pupate on the larval food-plant.

Why do males perch at some trees and not others? Females may prefer

certain trees as oviposition sites and therefore these trees are more likely to produce virgin females than others. We do not at this point know if females are more likely to oviposit on the trees preferred by males; we only know that females are more likely to appear there. It may also be that some trees provide better vantage points for looking for newly-emerged butterflies. We are currently testing this hypothesis by setting up large visual barriers and seeing if they affect male perch site selection.

Variation in Site Tenacity and Defense

Asterocampa leilia males fall somewhere in the middle of the spectrum of site tenacity and defense shown by male butterflies. Site tenacity and defense are typically closely tied. Some butterflies show essentially no site tenacity, such as the alfalfa butterfly (*Colias eurytheme* Boisduval). On the other hand, males of some species perch on and defend the same site during the activity period for several days (Davies, 1978; Suzuki, 1978; Lederhouse, 1982; Alcock, 1983, 1985; Knapton, 1985; Alcock & O'Neill, 1986). In *A. leilia* even the most attractive sites were occupied and defended for only a few consecutive 30 min census periods and rarely for more than one day. What ecological factors have favored this sort of behavior?

Site occupation and defense in butterflies is associated with mate location. Hence, the form of this behavior will depend on a complex interaction between the spatial and temporal distribution of receptive females and the density of competitors (Rutowski, 1984; Courtney & Parker, 1985; Odendaal et al., 1985; Alcock & O'Neill, 1986). Currently our understanding of this interaction awaits further detailed studies of mate-location in species that perch.

Spermatophore Size and Mating System Structure

Male butterflies expend energy in reproduction in two ways. The first is in mate location. The second is in making spermatophores which contain not only sperm but also accessory gland secretions that may be used by the female as nutrients for egg production (Rutowski, 1984). In species that engage in site defense we expect that the amount of effort put into site defense will be a major determinant of reproductive success. Although males that patrol also expend energy in mate location the cost of this can be ameliorrated by their ability to feed while searching for females. Vigilance during site defense precludes feeding and defended sites rarely contain nectar resources.

We predict, therefore, that in species in which males defend perch sites, the males will expend more on mate location and less on spermatophore production than in species in which the males patrol in search of mates. As expected, males of *A. leilia* (this study) and males of *Pararge aegeria* Linnaeus (Svard, 1985), another site defending species

(Davies, 1978; Wickman & Wiklund, 1983), produce spermatophores that are small in relation to their body weight (2-3%) compared with other species that have been examined. Rutowski et al. (1983) surveyed 10 species of butterflies in which males patrol in search of females and found that typically 6 to 7 percent of the male body weight was donated in each spermatophore. Further studies are needed to test the prediction that mating system structure is linked with the investment males make in nutrient contributions to their mates.

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The Biology of Seven Troidine Swallowtail Butterflies (Papilionidae) in Colima, Mexico

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Abstract. Observations on the early stages and ecology of the following aristolochia-feeding swallowtail butterflies are presented: *Battus philenor philenor* (Linnaeus), *B. polydamas lucayus* (Rothschild and Jordan), *B. eracon* (Godman and Salvin), *B. laodamas procas* (Godman and Salvin), *Parides photinus* (Doubleday), *P. montezuma* (Westwood), and *P. erithalion trichopus* (Rothschild and Jordan). Observations were made during 1979–1982 in the state of Colima, Mexico, by Paul Spade.
Resumen. Se presenta información sobre los estadios inmaduros y la ecología de los siguientes papiliónidos que comen aristolocáreas: *Battus philenor philenor* (Linnaeus), *B. polydamas lucayus* (Rothschild and Jordan), *B. eracon* (Godman and Salvin), *B. laodamas procas* (Godman and Salvin), *Parides photinus* (Doubleday), *P. montezuma* (Westwood), y *P. erithalion trichopus* (Rothschild and Jordan). Los datos fueron obtenidos durante 1979–1982 en el estado de Colima, México.

Introduction

Four species of *Battus* Scopoli are known from the state of Colima, Mexico: *B. philenor philenor* (Linnaeus), *B. polydamas lucayus* (Rothschild and Jordan), *B. eracon* (Godman and Salvin), and *B. laodamas procas* (Godman and Salvin). In the same region three species of *Parides* Hübner have been documented: *P. photinus* (Doubleday), *P. montezuma* (Westwood), and *P. erithalion trichopus* (Rothschild and Jordan). Both genera are confined to the New World, predominantly South America. *Battus* is the smaller, containing 14 species; *Parides* encompasses between about 32 and 45 species, 9 of which occur in Mexico.

Battus and *Parides* are members of the tribe Troidini (Papilionidae), commonly referred to as aristolochia swallowtails (Rothschild and

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Jordan 1906; Munroe 1960; Ehrlich and Raven 1965) because their larvae feed exclusively on members of the genus *Aristolochia* Linnaeus (Aristolochiaceae). This plant genus, composed primarily of tropical vines, can be divided into two natural groups in the Americas: pentandrous and hexandrous species (5 and 6 stamens respectively) (Pfeifer 1966, 1970). Table 1 outlines the major characteristics and distributions of *Aristolochia* species utilized by *Battus* and *Parides* in Colima.

Aristolochia species contain a number of secondary plant compounds including aristolochic acids, benzylisoquinoline alkaloids, and sesquiterpenoids, which in general deter both insect and vertebrate phytophagy (Fraenkel 1959). Some members of the Troidini are known to sequester these substances from their foodplants, rendering the butterflies distasteful to vertebrate predators. Consequently their colors are aposematically adapted (Brown, Damman and Feeny 1981). Hence adults are models in Batesian mimetic complexes involving butterflies of the same family in the genus *Papilio* Linnaeus (Brower 1958) and *Eurytides* Hübner. Various *Battus* and *Parides* species form Müllerian mimicry complexes as well (Young 1971a, 1971b, 1972; Brown, Damman and Feeny 1981).

The purpose of this paper is to present brief descriptions and illustrations of the early stages, summarize data on host utilization and geographic distribution, and identify the major mimetic complexes among the seven troidine swallowtails that occur in Colima, Mexico.

Methods and Study Area

The field work, including photography, was carried out by Paul Spade from November 1979 to November 1982. Specimens of both butterfly and *Aristolochia* species were sent by Spade to Hamilton Tyler who arranged for their determination. Voucher specimens of the butterflies were deposited in the San Diego Natural History Museum; no larvae were preserved. With the assistance of Michael Parsons, a preliminary draft of the present manuscript was completed. After the untimely death of Tyler, John Brown was responsible for the final organization and presentation of the paper.

Field work was conducted at 23 sites in Colima and 3 sites in the neighboring states of Michoacan and Jalisco (figure 1). Only the Colima localities mentioned in the text are shown in figure 1. All records of oviposition and hostplant selection are based on the discovery of eggs and larvae, or the observation of ovipositing females, in the field. Once located, the early stages were brought into the lab (Spade residence in Colima) and reared on the field-associated host at ambient temperature. All photographs were taken in the lab. No measurements of the early stages were noted as they were nearly identical, and most have been presented previously elsewhere (see literature citations in *Observations*).

Fig. 1.   Map of Colima, Mexico.

Colima is located along the western coast of mainland Mexico. Although one of the smallest states in the Republic, it is topographically extremely diverse; elevation ranges from sea level to nearly 3900 m at the peak of the Fuego Volcano. The Pacific shoreline, approximately 160 km long, is bordered by a narrow coastal plain. Low coastal ranges rise abruptly from the plain and quickly attain an elevation of 700—1300 m. Colima, the capital city, is located in the east-central part of the state on a dissected plateau which varies in altitude from 300—600 m. The interior mountain ranges rise to a nearly uniform elevation of about 2000 m.

According to Schaldach (1963), eight distinct vegetational zones occur within Colima, six of which are relevant to this study. These can be summarized as follows:

(1) **Arid thorn scrub**. A low, semi-open scrub community composed of spiny deciduous shrubs and legumes occurring along the coastal plain and the basal slopes of the coastal mountains.

(2) **Arid thorn forest**. A relatively tall (10—12 m), homogeneous forest of flowering trees, mostly legumes, found on hillsides and in many of the interior valleys. These deciduous forests are often dense with a thick undergrowth of thorny vines.

(3) **Riparian gallery forest**. Heavily shaded forests of tall, mainly evergreen trees, bordering all the permanant watercourses of the lower tropical area.

(4) **Tropical deciduous forest**. Tall, climax deciduous forest composed of many species of tropical trees; generally found above arid thorn

forest at higher, moister habitats, but may occur in lower elevations in response to local precipitation.

(5) **Oak woodland**. Nearly pure stands of low oaks found on the higher ridges of the mountains. Scattered pines occur amid the oaks, but nowhere do they form significant forests.

(6) **Arid pine-oak forest**. Open, dry forests of tall pines interspersed with medium-sized oaks, occurring primarily around the volcanoes from about 1800−2400 m. This is the highest habitat in which troidines occur in Colima.

Observations

Battus philenor philenor (Linnaeus)

Early stages. The early stages of *B. philenor* in Colima closely resemble those from elsewhere. First described by Edwards (1881), they are summarized in numerous accounts (e.g., Klots 1951; Emmel 1975; Opler and Krizek 1984; etc.); they are not illustrated here. The spherical egg is russet in color. First through third instar larvae are gregarious; later instars feed singly. The ground color of fourth and fifth instar larvae is usually dark purple with contrasting orange-red tubercles. However, a second color form also occurs in which the ground color is the same orange-red as that of the tubercles; the outer two-thirds of the anterior tubercles and the tips of both the longer thoracic and first abdominal tubercles, are tipped with black. This second color morph also occurs in southeastern Arizona populations of *B. philenor* (A. Shapiro, personal communication).

The pupae are dimorphic, as noted by West and Hazel (1979). One clutch of *B. philenor* yielded 15 brown, 3 green, and one mixed (brown and green) pupae. Thoracic projections of the pupae of *B. philenor* from Colima are less prominent than those from elsewhere.

Oviposition and foodplants. Eggs are laid in small batches of 4−6 on the undersides of the leaves of the foodplant, forming a well spaced group (as opposed to a close cluster). At Madrid, Colima, the preferred foodplant was *Aristolochia acontophylla*, on which larvae of *Parides montezuma* also were found. Where *A. acontophylla* was unavailable, the butterfly rarely utilized *A. tentaculata*. At higher altitudes, larvae occurred on *A. pringlei*. Many other species of *Aristolochia* are used by *B. philenor* in other parts of its wide geographic range; these are summarized by Scriber and Feeny (1976). Rausher (1980, 1981) provides data on host plant selection and temporal changes in oviposition preference.

Habitat and range. In the Colima region, *B. philenor* occupies relatively dry habitats receiving an annual precipitation of less than 1200 mm and characterized by a long dry season. *B. philenor* occurs from sea level to about 2400 m, reaching its upper limit in the arid pine-oak forests. In

western Michoacan, *B. philenor* was present on the coast at Placita and Aquila, but just inland, in the northern region near Zapotan, no adults were observed during a six-month period from June to November 1982. The species was common in regions of arid thorn scrub and arid pine-oak forest, but it was conspicuously absent from the humid forest above Colima (city).

Battus polydamas lucayus (Rothschild and Jordan) (figures 2, 8, and 14)

Early stages. The life history of this species has been recorded by Moss (1919), Comstock and Vazquez (1960), Young (1971a), and Brown, Damman, and Feeny (1981). Eggs (fig. 2) are pale brown bearing 10 – 12 orange-brown vertical ribs of a glue-like colleterial substance that adheres them to the leaf of the foodplant.

The first instar larva is pale straw yellow; the short, hirsute tubercles bear long black setae. The second instar is brown-black, sparsely marked with tan-brown; the tubercles are light brown except those of abdominal segments 3 and 7, which are orange. The third instar is tan-gray with contrasting transverse, oblique, brown lines on each segment. The tubercles have a light brown base and darken towards the apex; the lateral tubercles are twice the length of the dorsal ones. The fourth instar larva is gray with thin, black transverse lines. All of the tubercles are cream-white with black tips, except the lateral tubercles, which are black with a cream base. The fifth instar is dimorphic. The pale form (fig. 8) is yellow-brown and resembles the fourth instar, while the other form is dark brown with black transverse lines, and black-tipped pink tubercles. The base of the lateral prothoracic tubercles is pale pink in the dark form, creamy yellow in the light form.

The pupae are dimorphic: one form (fig. 14) is green with pale yellow saddle and antennae, the other form brown. The pupa has a prominent, conical, dorsal thoracic projection, and the abdomen bears two prominent dorsolateral ridges.

Oviposition and foodplants. Females typically lay eggs in small clusters of 2 – 9 in a band around the stem of the host. In Colima, larvae were found on *Aristolochia acontophylla, A. foetida, A. odoratissima, A. tentaculata*, and *A. conversiae*.

Habitat and range. *B. polydamas* is the most common troidine in Colima. Throughout its range in the State it occupies primarily open habitats such as agricultural land, gardens, and arid thorn scrub; but it also occurs in riparian gallery forest. It is common from sea level to about 500 m, ranging as high as 900 m. An exceptionally high elevation record for this species in Colima is 1360 m at Cofradia de Suchitan.

Battus eracon (Godman and Salvin) (figures 3, 9 and 15)

Early stages. There are no details of the life history of this species in the literature. Eggs (fig. 3) are pink with irregular rib-like globules of
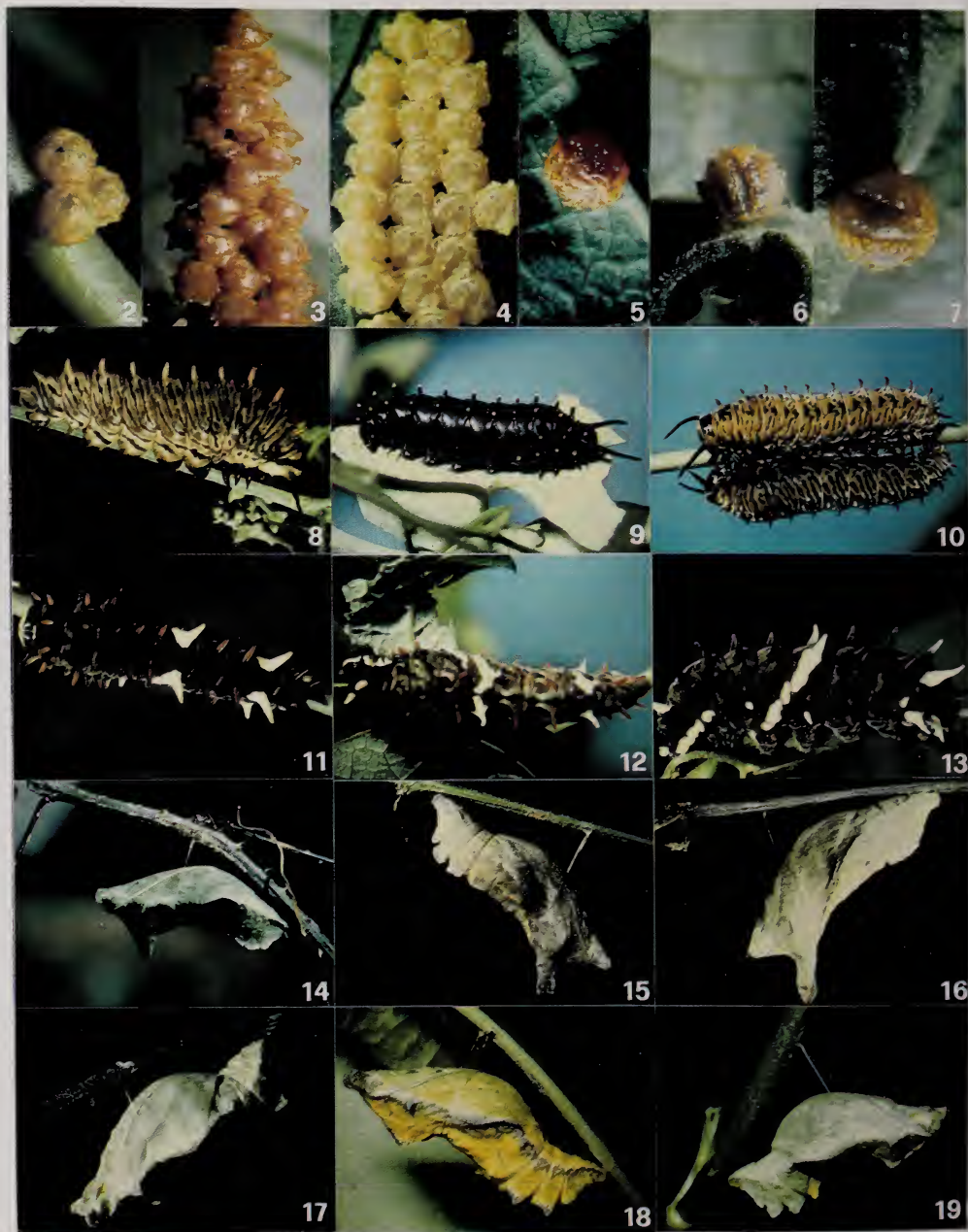
Figs. 2–7.   Eggs of *Battus polydamas* (2); *B. eracon* (3); *B. laodamas procas* (4); *Parides photinus* (5); *P. montezuma* (6); and *P. erithalion trichopus* (7).

Figs. 8–13.   Last instar larvae of *Battus polydamas* (8); *B. eracon* (9); *B. laodamas procas* (10); *Parides photinus* (11); *P. montezuma* (12); and *P. erithalion trichopus* (13).

Figs. 14–19.   Pupae of *Battus polydamas* (14); *B. eracon* (15); *B. laodamas procas* (16); *Parides photinus* (17); *P. montezuma* (18); and *P. erithalion trichopus* (19).

orange glue-like colleterial secretion which binds each egg within the batch and gives them a warty appearance.

Unfortunately, field collected eggs were eaten, presumably by ants, so first and second instar larvae were not obtained. Subsequent field collected larvae were all in later instars. Third instar larvae are chocolate brown with only the tips of the tubercles orange; the lateral prothoracic tubercles are concolorous with the body and much longer than the rest. Of the four species of *Battus* in Colima, *B. eracon* has the shortest tubercles. The fourth instar is indistinguishable in pattern from the third, but its ground color is maroon-brown. Fifth instar larvae are dimorphic: the dark form (fig. 9) is the most common and is almost entirely purple-black; only the tubercles are orange-tipped. The pale form is brown with oblique brown-black markings similar to those of *Battus polydamas*, with the lateral prothoracic tubercles entirely black. In both forms the head and thoracic prolegs are black. The first three instars probably feed gregariously, later instars feed singly.

The pupae are dimorphic: one form is green and yellow, the other (fig. 15) brown with greatly reduced yellow markings. Pupae average 37 mm long and 20 mm wide, with a dorsal thoracic projection of about 5 mm, more club-shaped than that of *B. laodamas procas*.

Oviposition and foodplants. A single female was observed ovipositing. Eggs were irregularly piled in batches of 20−30, near the ground, on the sides of stems supporting the foodplant, *Aristolochia tentaculata*.

Habitat and range. B. eracon is the most restricted mainland *Battus*, limited to the coastal regions of Colima, Jalisco, Michoacan, and Guerrero, Mexico (Hoffman 1976; Diaz Frances and de la Maza 1978). It is common between sea level and 200 m, where its range includes the coastal hills at Caleras. In Colima, *B. eracon* is locally abundant at Cerro de la Vieja (near Coquimatlan) and Tepames; both localities are about 500 m in elevation. It has not been observed above 610 m. In Michoacan, *B. eracon* occurs at Placita, Aquila, San Telmo, and Zapotan. Its principal habitats are riparian gallery forest, arid thorn forest, and tropical deciduous forest; adults are avidly attracted to nectar sources within these habitats. It is scarce in urban and arid thorn scrub areas.

Battus laodamas procas (Godman and Salvin) (figures 4, 10, 16)

Early stages. Comstock and Vazquez (1960) described the final instar and pupa of this species. Eggs (fig. 4) are pale yellow with six irregular vertical, rib-like strands of glue-like colleterial substance of the same color.

First instar larvae are light brown with black-tipped tubercles bearing long setae; the head is shiny black. Second, third, and fourth instar larvae are entirely black. Two distinct forms and intermediates are exhibited by fifth instar larvae: one form is entirely black, the other (fig. 10) is light brown with oblique black markings similar to those of *B.*

polydamas. In the brown form the tubercles are black-tipped. All instars feed gregariously.

The pupae are dimorphic with a green and yellow form, and a gray-brown form (fig. 16) that has greatly reduced yellow markings. The abdominal tubercles are reduced, forming two dorsolateral ridges.

Oviposition and foodplants. Eggs are laid in parallel rows in batches of 20–30 on the upper surface of leaves of *Aristolochia tentaculata*. Oviposition is generally between 3–4 m above the ground and always above 2 m.

Habitat and range. *B. laodamas procas* has the same distribution as *B. eracon* along the Pacific coast, but ranges further inland and into higher altitudes. It is most common from sea level to about 500 m. However, in the mountains it has been recorded as high as 1280 m.

Parides photinus (Doubleday) (figures 5, 11, and 17)

Early stages. The life history of *P. photinus* has been described in detail by Ross (1964). The following descriptions are based on observations in Colima. The egg (fig. 5) is dark pink with about 15 irregular, warty, vertical strands of yellow-orange colleterial secretion. Each egg rests on a short pedestal of the same substance, to one side of the base.

First instar larvae are gray with the dorsal tubercles of abdominal segments 4 and 7 pale yellow, and the thoracic and anal two pair of dorsal tubercles pale orange. The remaining tubercles are burgundy. Second instar larvae are darker; dorsal tubercles four and seven are creamy white. The thoracic tubercles and those at the anal end of the abdomen are pink. The third instar is dimorphic. The lighter form is similar to the preceding instar, but the dorsal tubercles on abdominal segments 4 and 7 are ivory-white. An oblique white line joins tubercle four with the lateral tubercle on abdominal segment 3 which is also ivory-white. The thoracic tubercles and the two pair of dorsal tubercles on the last abdominal segment are creamy orange, tipped with orange-red. The dark form is similar but the lateral and dorsal tubercles on abdominal segments 4 and 7 are ivory-white with a white stripe joining those on segment 4. All of the remaining tubercles and the ground color are dark red. First through third instar larva bear black setae at the tips of the tubercles. The fourth instar is also dimorphic, the two forms similar to those of the third instar The fifth instar is dimorphic: one form (fig. 11) is black with white and red tubercles which have an orange cast; the other is purple-black with dark red tubercles.

The pupa (fig. 17) is pale yellow dorsally and pale green ventrally. It has two short, triangular, dorsolateral processes on the thorax, and the abdomen bears a row of three pairs of triangular-shaped dorsolateral projections.

In Colima, the duration of the early stages is fairly rapid: egg, 6 days; first and second instar, 3 days; third instar, 3 days; fourth instar, 2 days;

fifth instar 3 days, prepupa to eclosure, 18−20 days. In *Battus* and *Parides* species studied by Brown, Damman, and Feeny (1981), larvae developed in 20−30 days. They suggest that in addition to temperature, developmental rates dependent greatly upon the species of *Aristolochia* utilized.

Oviposition and foodplants. In low to mid-elevations *Aristolochia tentaculata* is the larval host. At slightly higher elevation *A. conversiae* is utilized. In the vicinity of the Nevada de Colima Volcano, Jalisco, just north of the Fuego Volcano, the host is *A. pringlei*. Eggs are laid singly on the leaves.

Habitat and range. In Colima, *P. photinus* was observed in lower arid thorn forests at about 400 m, in oak woodlands at about 1680 m, and in arid pine-oak forests at 2400 m. It seems to favor forest margins and areas of disturbed or secondary vegetation. *P. photinus* exhibits the greatest altitudinal range of any of the Colima troidines except for *B. philenor*.

Parides montezuma (Westwood) (figures 6, 12, and 18)

Early stages. There are no details of the life history of this species in the literature. The egg (fig. 6) is pale gray-brown with about 12 irregular, warty, vertical rib-like strands of yellow colleterial substance. The egg rests on a pedestal of colleterial substance which is shorter than that of *P. photinus*.

First instar larvae have a pinkish yellow ground color with yellow-orange tubercles that bear long gray setae. The head is tan-brown. The second instar larva is dark gray with the tubercles light orange except for the dorsal ones of the mesothorax and abdominal segments 4 and 7, which are white. The third instar is white with the tubercles red-orange except for the lateral ones on the meso- and metathorax, and on abdominal segments 3 and 7, which are white. There are oblique gray-brown stripes laterally on each segment. The fourth instar is similar in pattern, but the white tubercles are highlighted by a more extensive pattern of darker brown stripes. The remaining tubercles are red. The head and thoracic prolegs are black. In the fifth instar (fig. 12) the ground color is gray-black, with numerous oblique black stripes, the white tubercles strongly contrasting. The remaining tubercles are burgundy. Both the ground color and tubercle color exhibit a narrow but conspicuous range of variability in the fifth instar.

The pupa (fig. 18) is yellow with a lavender-gray lateral abdominal band that continues onto the wings and the lateral tubercles of the mesothorax. The same color forms a midline dorsally along the thorax, continuing onto the frontal tubercles and those of the abdomen as well. The dorsal saddle of the abdomen has a pink midline and two fine dorsolateral lines of gray. Ventrally the wings and legs are greenish yellow.

Oviposition and foodplants. Eggs are always laid singly on the undersides of leaves of the foodplant or on the tips of new vegetative shoots. Ovipositing females are easily followed as they exhibit a slow, fluttering flight close to the ground. Eggs are never deposited higher than 1.5 m above the ground. At Estapilla, in arid thorn scrub, a female was observed ovipositing on an *Aristolochia acontophylla* plant which was only 15 cm tall. The same species of foodplant is utilized at Zapotan and Madrid. In the latter locality *P. montezuma* also was observed ovipositing on *A. foetida*, although no larvae were ever encountered on this species. At Madrid an undescribed species of *Aristolochia* was available, but never utilized by *P. montezuma*. Eggs of *P. montezuma* were found once on *A. cardiantha*. At higher elevations *A. conversiae* is utilized.

Habitat and range. P. montezuma is generally common throughout its range from sea level to about 1360 at Cofradia de Suchitan, occupying a variety of habitats including arid thorn and tropical deciduous forests. Unlike *P. photinus, P. montezuma* does not occur in the arid pine-oak forest.

Parides erithalion trichopus (Rothschild and Jordan) (figures 7, 13, and 19)

Early stages. An outline description of the early stages of this species was presented by de la Maza (1980). The egg (fig. 7) is pale gray with about 12 irregular, warty, vertical rib-like strands of orange glue-like colleterial secretion. Eggs are laid singly on the underside of leaves of the foodplant, and rest on a short pedestal of colleterial substance to one side of the base. The glue-like strands are more granular in appearance than on the eggs of either *P. montezuma* or *P. photinus*, and the pedestal is shorter than in those two species.

The first instar is orange-yellow except for the mesothoracic tubercles and the dorsal tubercles of abdominal segments 4, 7, and 9, which are translucent white. The prothoracic shield is gray-brown and the head is shiny black. The second instar is yellow-gray with the lighter tubercles brighter white. The lateral tubercles of the prothorax, metathorax, and abdominal segments 7 and 9 are also white. The remaining tubercles are translucent orange-yellow. In the third instar the ground color is reddish brown, the darker tubercles pinkish red. The lateral tubercles of abdominal segments 7 and 8 are white. The fourth instar is similar, but the ground color and darker tubercles are burgundy, and the white tubercles on abdominal segments 3 (lateral) and 4 (dorsal) are joined by an oblique white stripe. The tips of the dorsal tubercles on abdominal segment 5 are white. In instars one through four, the tubercles bear setae. These are longest on the first instar and decrease in length at each successive molt. Fifth instar larvae are dimorphic: one form (fig. 13) is gray-black, the other dark brown. Both are marked with oblique

charcoal-black lines. The white of the lighter tubercles is quite exten-
sive and gives the larva a clearly defined anterior, median, and posterior
pattern of lines and spots.

The pupa (fig. 19) is greenish gray; the dorsal region, the saddle of the
abdomen, and the cremaster are yellow. The dorsolateral tubercles of
the abdomen are broad and triangular in profile.

Oviposition and foodplants. Females exhibit a slow, low, fluttering
flight while searching for foodplants. Eggs are laid singly on the
underside of leaves of the host, or occasionally near the tips of new
shoots. At Tamala, La Salada, Madrid, and Caleras, *P. erithalion*
utilizes an undescribed, deciduous species of *Aristolochia*. Other hosts
documented from the lowlands include *A. tentaculata* and *A. mutabilis*.
Aristolochia conversiae is assumed to be the host at mid elevations (e.g.,
San Antonio and Tonila) where it is the only potential foodplant
available.

Habitat and range. *P. erithalion trichopus* is limited to western
Mexico. In Colima it has been observed from sea level to 1520 m, but this
may not be its upper limit. The species was abundant in arid thorn
forest, less common in arid thorn scrub. With the exception of large
urban areas, *P. erithalion* was fairly common in all habitats.

Mimetic Associations of Adults

In Jalisco, *Battus philenor* and *Parides alopius* (Godman and Salvin),
both assumed to be unpalatable, form a Müllerian mimetic complex. In
Colima, *B. philenor* is the model for the palatable *Papilio polyxenes
asterius* Stoll, a Batesian mimic over much of their extensive concurrent
geographical ranges. *B. polydamas, B. laodamas,* and *B. eracon* are
assumed to be unpalatable, and comprise a Müllerian mimetic complex
in Colima, in which *B. polydamas* is the most common species. Also
associated with these species are the Batesian mimics *Papilio victorinus
morelius* Rothschild and Jordan, which is common, and females of
Papilio astyalus Godart, a population similar to *P. astyalus occidentalis*
Brown and Faulkner, which are uncommon. Females of *Papilio an-
drogeus epidaurus* Godman and Salvin also may be Batesian mimics of
the *Battus* complex.

The three *Parides* species in Colima form their own Müllerian
mimetic complex, again assuming unpalatability. *Papilio pharnaces*
(Westwood), *P. anchisiades* Esper, *Eurytides thymbreus aconophus*
(Gray), and *E. belesis* (Bates) are Batesian mimics of the *Parides* group,
the former representing an extraordinary convergence to *Parides* in
both coloration and pattern. The nymphalid butterfly *Biblis hyperia*
(Cramer) is also a Batesian mimic of *Parides* in Colima.

Conclusions

Table 2 summarizes the field data of foodplant utilization by Troidini

Table 1.   Characteristics and distribution of *Aristolochia* species in Colima, Mexico.

species	hexandrous/ pentandrous	growth habit	size	habitat	elevations in Colima	general distribution
A. tentaculata Schmidt	hexandrous	glabrous small lianas	large; to 7 m	widespread	common to 800 m; sparse 800-900 m; pockets to 1036 m	Colima, Michoacan, Guerrero, D.F.
A. glossa Pfeifer	hexandrous	glabrous lianas	very large	riparian	0-250 m	Colima and Michoacan
A. odoratissima Linnaeus	hexandrous	glabrous lianas	large	riparian	0-250 m	Mexico to Panama
A. n. sp	pentandrous	dwarf herb	small; 2.0-2.5 m	rocky hillsides	0-250 m	unknown (Colima)
A. acontophylla Pfeifer	pentandrous	sprawling herbaceous perennial	small; less than 1.0 m	open sunny areas in thorn forest	below 300 m	Colima and Michoacan
A. cardiantha Pfeifer	pentandrous	procumbent perennial herb	small; 2.0 m ±‑	thorn forest	ca 1000 m	Colima, Guerrero, Mexico D. F.
A. foetida H. B. K.	pentandrous	procumbent perennial herb	small; less than 1.0 m	thorn forest	200-1128 m	Jalisco, Colima, Michoacan, and Guerrero
A. conversiae Pfeifer	pentandrous	procumbent perennial herb	small	pine-oak, tropical deciduous	960-1740 m	Colima, Mexico D.F.
A. pringlei Rose	pentandrous	twining perennial herb	small	moist meadows in pine-oak forest	2285 m	Nayarit, Jalisco, Morelos, and Michoacan
A. mutabilis Pfeifer	pentandrous	procumbent perennial herb	small	thorn forest	0-250 m	Colima, Michoacan, and Guerrero

Table 2.   Summary of foodplant utilization by Colima Troidini.

	philenor	polydamas	eracon	laodamas	photinus	montezuma	erithalion
A. tentaculata	+	+	+	++	++		+
A. glossa			?	?			
A. odoratissima		+	?	?			
A. n. sp.							+
A. acontophylla	++	+				++	
A. cardiantha						+	
A. foetida		+	?			+	
A. conversiae		+			++	++	?
A. pringlei	++				+		
A. mutabilis							+

++ = preferred foodplant (4 or more observations)
+ = documented foodplant (1−3 observations)
? = possible foodplant (most likely available host; no observations)

in Colima, Mexico. *Aristolochia tentaculata* is an important foodplant to nearly all the species studied. K. Brown (personal communication) suggests that the relative toxicity of different species of *Aristolochia* varies, and that the first choice of foodplant would be the least toxic species available. Where troidines occur in sympatry, there may be competition for such a foodplant. In the absence of specific biochemical data on plant secondary compounds, *A. tentaculata* is suspected to represent such a species in Colima.

From this study *Battus eracon* and *B. laodamas procas* appear to be monophagous, although this may not be the case. It is possible that both species utilize all three of the large hexandrous *Aristolochia* species available. *B. polydamas* is the most polyphagous troidine; it successfully utilizes five species of *Aristolochia* in Colima.

There is no unequivocal evidence from the data or observations that Colima troidines are partitioning hosts to avoid interspecific competition, but this is implied by regional shifts in foodplant choice. Where, for example, several troidines are sympatric, host utilization seems to differ from allopatric situations. Partitioning by *Battus* and *Parides* between hexandrous and pentandrous species of *Aristolochia* in Colima is also suggested. Pentandrous species are small, usually only 1–2 m in height; hexandrous species are typically much larger (table 1). *Parides* species lay their eggs singly (Brown, Damman, and Feeny 1981); females usually search at ground level. *Parides* thus are able to exploit small, low-growing pentandrous species. In contrast, *Battus* species typically lay eggs in batches. Gregarious larvae soon devour small foodplants and have to search for additional host material. Survival is possible on pentandrous species only where close growing stands occur. In general, *Battus* species would seem to have greater survival and face less intraspecific larval competition on large hexandrous species, where ample foodplant is available for large numbers of actively feeding larvae. This assumption is supported by the fact that *B. eracon* and *B. laodamas* were observed to feed exclusively on the large hexandrous *A. tentaculata*. Evidence to the contrary includes the preference for pentandrous species exhibited by *B. philenor*, which is moderately polyphagous, and the inability to determine preference of *B. polydamas*.

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The Mating Behavior of *Papilio glaucus* (Papilionidae)

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Abstract. Male and female *Papilio glaucus* were released in a large flight cage containing vegetation simulating a forest clearing. Observations were made to study courtship behavior and the mating system of *P. glaucus*. Mechanisms of female choice through solicitation of males and rejection behavior during courtship are presented.

Introduction

The tiger swallowtail, *Papilio glaucus* L., has monomorphic non-mimetic males as well as two female forms: one male-like and the other a Batesian mimic of *Battus philenor* L. It has therefore been of interest in studies of assortative mating (Burns, 1966; Platt, Harrison and Williams, 1984) and sexual selection in mimetic species (Brower, 1963; Silberglied, 1984; Krebs, 1986). Despite this general interest, little information is available on its mating behavior. This note describes courtship and mate avoidance behaviors in *P. glaucus* and suggests mechanisms for female choice.

Materials and Methods

Adults were reared from eggs of field-caught females (Virginia) and females sent by Mark Scriber, University of Wisconsin (Wisconsin and Illinois), for experiments in 1984 and 1985. Although geographically variable, all butterflies used were *P. glaucus glaucus*. Larvae were reared on fresh black cherry leaves (*Prunus serotina*) in the laboratory under a long photoperiod to prevent diapause which allowed rearing of three generations.

The experimental population for 1985 was produced by randomly crossing field-caught, Wisconsin, and Illinois butterflies early in the experiment and rearing and crossing these offspring throughout the summer. Observations therefore began with pure strain individuals presented at random and continued with offspring of geographically mixed parentage. Observations made in the Spring of 1984 included only reared Blacksburg individuals.

Observations were made in a flight cage (5 × 8 × 5 m) in Blacksburg, Virginia. The cage resembled a forest clearing with small trees, including *Prunus serotina*, inside. Vines lined the sides and larger trees surrounded the cage.

Because an outdoor cage was used, weather conditions could not be controlled. All observations were made between noon and 4:30 PM on days ranging in temperature from 22 to 33°C. Temperatures outside this range, high winds and cloudy conditions decreased flight too much to allow for efficient testing.

A single virgin female, 1 to 3 days old, was released to one male, 2 to 4 days old.

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Observations were made until either several unsuccessful courtships or a mating occurred. The average observation time was one hour per pair.

Results

General

A total of 196 courtships using 70 *P. glaucus* pairs (17 in 1984 and 53 in 1985) was observed. Of these, 34 (17%) led to matings. Because results were similar when either Virginia butterflies were presented to each other (1984) or the geographically mixed populations (1985) were used, structure of successful courtships versus unsuccessful ones for all presentations are grouped when discussed below.

Successful courtships

Typical courtships leading to copulation involved an exchange of behaviors in flight between males and females. These flights were initiated when responsive males encountered females, usually in air (27 of 34) or on vegetation (6 of 34). Within the cage, males usually initiated courtship. However, in nine courtships leading to copulation, females flew toward the male, soliciting courtship. One such flight was directed to a male on vegetation.

Following initial interactions, females flew up and away from males which pursued 5-15 cm below and behind. Most of these courtship flights therefore occurred along the cage top at 5 m. In two observations butterflies released in the field ascended into and over tree tops and out of sight.

Courtship flights were highly variable in length ($\bar{x}$ = 16.5 s ± 3.9 s, n = 18, range 0-59 s). However, only 7 of 34 matings occurred after the first courtship. Total courtship flight time preceding copulation averaged 58 ± 12 s (n = 18). Successful males averaged 2.6 courtships (n = 34) before they were accepted by females.

Pursuit flights continued until the females landed with wings either open (7 of 31) or closed (24 of 31). The male hovered above the female for a second or two before attempting to land beside her (23 of 34), but sometimes (11 of 34) immediately landed by the female. When a female landed with open wings, the male always hovered. Wing closing by a female was quickly followed by the male alighting beside the female.

Three courtships leading to mating lacked usual courtship flights. In those, the males hovered over the females perched on vegetation, landed and were accepted. However, courtship flights had occurred previously in all three.

A male, once beside the female, extended his abdomen to contact the female's genitalia. After acceptance, he relaxed, dropped below the female and remained stationary in copula for 45 min to an hour. Most matings occurred along the cage top, with only a few as low as three

meters. No post copulatory flights were observed unless the pair was disturbed. In flight, females flew with males hanging below.

Unsuccessful courtships

Unsuccessful courtships were ended by either males or females. Of 162 unsuccessful courtships, designated as those interactions between males and females which lasted at least a second, 33 encounters in air never led to a pursuit flight. These interactions ended when males failed to respond to females (26 males, not included in the above total, never courted females presented to them).

Of the other 129 courtship flights, 104 broke up while males were pursuing females. The remaining 25 ended after males interacted with perched females. Because these males were responding positively to females, failure to mate was probably due to behaviors on the part of females to evade or reject courting males.

Unsuccessful courtships lasted longer than those that ended in copulation ($\bar{x}$ = 103 ± 15 s, n = 18, p<0.02). Number of courtships, however, did not differ, 2.72 ± .21 for unsuccessful males and 2.56 ± .26 for successful ones (p>0.3).

Discussion

Several aspects of *P. glaucus* mating behavior are very different from that of other species. Most notable is the high incidence of courtship solicitation by females. Solicitation flights were generally made directly to males in flight, although perching males were also solicited. Females flew across either from the side or above males within 15 cm, turned, and flew up and away. If males failed to pursue, solicitation was often repeated.

Solicitation flights have also been observed in *Pieris protodice* Boisduval and LeConte (Rutowski, 1980), *Heliconius erato* L. (Crane, 1955), *Danaus gilippus* Cramer (Brower, Brower and Cranston, 1965) and *Aphantopus hyperanthus* L. (Wicklund, 1982). In *P. glaucus*, solicitations were observed for 53% of males that mated; 9 of 34 matings had been immediately preceded by solicitation. Thirty-seven percent of all first interactions between males and females were initiated by females. Also, of 26 males that were not responsive to females, 85% received solicitations.

A second unusual feature of *P. glaucus* courtship is lack of antennal contact between males and females. Brower et al. (1965) described males of *D. gilippus* brushing antennae of females with specialized scent scales. Scent is important in courtship to many other butterfly species (Thornhill and Alcock, 1983). However, as *P. glaucus* males court from below and behind females, some wing contact occurs from below but none near the female's head. Opportunity to pass scent did occur when females landed but only occasional wing contact was observed before the

male attempted to land and copulate. These behaviors suggest that visual cues are far more important than olfactory in mate choice in this species.

With only 17% of all courtships with virgin females leading to matings, females are able to reject and avoid males. Longer courtship times of unsuccessful males suggested that females avoided landing until pursuing males were evaded.

Two observed avoidance postures were closing and depressing the wings when a male flew near, and depressing the abdomen to the substrate to avoid genital contact when a male landed. Rejection behaviors during pursuit included "quick landing," a sudden stop with wings closed and depressed, and "dropping," a relaxed free fall into brush. Females also employed slow descending flights, which forced males to abandon courtship when females hovered less than 30 cm above the ground. Two less obvious behaviors were flying through thick brush, also observed in *D. gilippus* (Brower et al. 1965), and simply not flying, a behavior I observed when females were released with a high male density. Virgin females have been observed to reject males by like means in other species (Rutowski, 1982, 1984).

Comparisons in this study suggested no differences between male responses to the two female forms, mimetic and male-like. While the experimental design did not provide for controlled comparisons of details within courtship flights, overall mating success and male courtship frequency were not different.

One question in this study is its application to mating behavior in nature. Only two courtship flights, described earlier, were observed outside of the cage, although releases, albeit unsuccessful, were attempted. However, vegetation within the cage, and its size, provided more natural conditions than in most other cage studies.

Brower (1963) says that *P. glaucus* males fly around courting any females located. No other description of a mating system exists for this species, and no territorial behavior is known. Multiple male releases in the cage elicited no male-male interaction. Attempts by several males to court the same female simultaneously were observed. None were successful. Only in mudpuddling aggregations are high densities of males found.

Rutowski (1984) suggests that prolonged searching polygyny is the most likely mating system to be found in butterflies. Strong rapid flight, lack of male-male competition and dispersed abundant food and oviposition sites suggests the existence of this system in *P. glaucus*.

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A New Heritable Color Aberration in the Tiger Swallowtail Butterfly, *Papilio glaucus* (Papilionidae: Lepidoptera)

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Abstract. A new wing color aberration in the Eastern tiger swallowtail, *Papilio glaucus* L., has been discovered and is called "dark cell". This dark scale suffusion into the dorsal forewings has a genetic basis and appears restricted to females. We describe the new aberration and our attempts to rear offspring of hand-pairings for elucidation of the genetic basis of the trait.

Introduction

A number of wing color aberrations in *Papilio glaucus* L. have recently been described by Clark and Clark (1951), Clarke and Clarke (1983) and Scriber et al. (1987). Here we report a new wing color aberration in *Papilio glaucus* L. which is apparently genetically based and sex-limited in expression. Following the first appearance of this aberration (which we call "dark cells") in our 1982 laboratory cultures, we hand-paired (sibs) in an attempt to elucidate the genetic basis of the character.

Methods

Oviposition by adult females was induced by placing each wild-captured or hand-paired female into its own clear plastic box (approximately 10 cm deep × 15 cm × 30 cm) with a moist paper towel and selected larval foodplant leaves. Leaf turgor was maintained in these plants by use of floral aquapics® (water-filled plastic vials with a rubber cap, through which leaf petioles or small branches can be inserted; see Scriber, 1977). Heat and light were provided by an incandescent bulb placed at a distance of approximately 0.3-0.5 meter from the plastic boxes.

Larvae were reared through to pupation on black cherry, *Prunus serotina* Ehrh., or another foodplant (leaves were changed three times per week) under controlled environment conditions (16:8 photo-/scotophase with corresponding temperatures of 23.5°/19.5°C, respectively).

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Pupae were weighed 2 days after pupation (the weight subsequently serving as an identification number for the individual) and then placed in cylindrical screen cages (15 cm diameter × 12 cm height) under larval rearing conditions to permit development and eclosion as adults. Non-diapausing individuals normally emerged within 2-3 weeks after pupation. Other pupae were allowed at least 6 weeks before being refrigerated in darkness (at 40-45°F for 3 months or more) to break diapause. Hand-pairings were generally attempted 12-48 hrs after adult female eclosion and 2-3 days after male eclosion.

Results

We first observed our new color aberration in females of a 1982 lab-reared brood (#56). We term this aberration "dark cell" because of the abnormal suffusion of dark scales into the normally yellow cells of the forewings (Fig. 1). Brood #56 was the result of a yellow morph mother (a virgin *P. g. glaucus*, 3rd generation lab-reared, originally from stock collected in 1981 from Schuylkill County, Pennsylvania by William Houtz) which was mated to a male whose mother was also from this PA stock but whost father was a subspecies hybrid (from a *P. g. canadensis* female from Clarke Co., Wisconsin mated to a *P. g. glaucus* male from Pennsylvania).

Crosses #290 and #296 (Table I) are both crosses from a "dark cell" daughter and one of her male siblings (all from brood # 56). It can be seen that this dark cells trait occurs only in the females. The four siblings shown here (Fig. 1) represent some of the variation in the "dark cell" trait.

The origin of this character, and the genetic basis of its expression are difficult to decipher because of the complexity of the parental lineages, and the fact that no livestock currently exists from this lineage (brood #56, #290, or #296). Only two additional related females were hand-paired: one with a *P. g. glaucus* from Richland Co., Wisconsin (brood #299; see Table 1), and the other produced no eggs.

While checking the results of our 1982-1986 hand-pairings, lab rearings, and field captures, we discovered a total of 5 additional "dark cell" phenotypes in our research collection (> 25,000 butterflies). Each of these individuals resulted from a subspecies pairing involving a *P. g. canadensis* male parent, and each also emerged in 1984 from hand-pairings done in 1982. The first was one of 13 female progeny (19 male progeny) from a dark male *P. g. glaucus* from Georgia meted to a *P. g. canadensis* from northern Wisconsin (pairing #39). A second was one of 4 female progeny (9 male progeny) of a lab-reared yellow *P. g. glaucus* female (from Pennsylvania parents) mated to a *P. g. canadensis* from Bayfield County, Wisconsin (pairing #116). The third and fourth were female siblings out of a total of 7 females (4 male sibs) from a yellow lab-reared *P. g. glaucus* female (from Pennsylvania parents) mated to a *P. g.*

Table 1.   Adult phenotypes[1] from laboratory crosses. Madison, Wisconsin (1982)

Mother number	Pairing Background (female × male)	Larvae/ total eggs	Number of Male Offspring	Number of Female Offspring	
				"Normal" yellow	"Dark cell"
Female #56	(#71 × #H15)	74/132	8	3	9
Female #290*	(#56 × #56)	172/391	15	8	7
Female #296	(#56 × #56)	201/271	18	1	22
Female #299	(#56 × *P. g.*)	190/208	13	6	0

[1]The "dark cell" aberration was first detected in offspring of female #56. Two fertile sibling-sibling pairings (290 and #296) both resulted in some "dark cell" phenotypes, differing from #299. One additional daughter from #56 was mated (female #537) but produced no eggs. No other pairings were made from the female #56 lineage.
*One deformed pharate female was not able to be classified.

canadensis from Juneau County, Wisconsin (pairing #144). The final "dark cell" phenotype was a female from a yellow lab-reared *P. g. australis* female from Florida, mated to a *P. g. canadensis* from Bayfield County, Wisconsin (pairing #115). Only one living pupa from these lineages currently exists.

Discussion

   Sir Cyril Clarke and colleagues have been investigating the genetic basis of abnormal wing coloration in *Papilio glaucus* for decades (see Clarke and Clarke, 1983 for a review). They point out that color mosaics and gynandromorph *P. glaucus* can be striking, because of the contrast between the yellow background (of males and yellow morph females) against the black/brown melanic background of the dark morph females

Fig. 1.   Four female siblings (of 22 "dark cell" produced in brood #296) exhibiting variations of our "dark cell" aberration: Left, dorsal; Right, ventral. This aberrant was originally detected in the parental brood (#56; see text and Table 1)
      A) pupal weight 0.8720 g; eclosed 29 Sept. 1982
      B) pupal weight 1.1946 g; eclosed 29 Sept. 1982
      C) pupal weight 1,6900 g; eclosed 23 Sept. 1982
      D) pupal weight 1.2956 g; eclosed 20 Sept. 1982

These dark/yellow gynandromophs and color mosaics are quite rare, and considerable attention has been given to existing specimens. For example, the Herman Strecker collection (currently on loan from the Chicago Field Museum to the Allyn Museum in Florida) contains a number of such mosaics. This valuable collection, assembled during the second half of the 19th century, contains a number of *P. g. glaucus* mosaics previously discussed in the literature (Strecker, 1878; Ehrmann, 1894; Howard, 1899; Walsten, 1977; Ehle, 1981; Shapiro, 1981b Clarke and Clarke, 1983). The Milwaukee Public Museum (Milwaukee, Wisconsin) also contains (in the Neidhoefer collection) two partial color mosaics reared by E. Dluhy in Chicago, Illinois. Color mosaics also exist from Richmond County, NY (5 July 1971; A.M. Shapiro; currently in the University of California Davis Collection) and from Washington County, PA (9 May 1927; George F. Patterson Collection at Pennsylvania State University).

Scriber and Evans (in press) describe an additional two dozen color mosaics from *Papilio glaucus* (see also Scriber et al, 1987); however, in the investigation of this entire group of color aberrations and in investigations of *Papilio glaucus* from (many) institutional and personal collections (see Scriber and Evans, 1986b), we have never encountered material similar to the "dark cell" aberration *P. glaucus* females described here (Fig. 1).

We are aware of the superficial resemblance of "dark cell" to the melanic aberration "fletcheri" in males of *P. g. canadensis*, and we have reviewed the literature and figured this form from Wisconsin previously (Scriber and Lintereur, 1983). The "fletcheri" aberration has been noted several times from northern Wisconsin (Ebner, 1960; Scriber and Lintereur, 1983; and W. Gould, J. Trick, D. Robacker, D. Matusik pers. comm.) and it is possible (though we consider it remote) that there has been introgression from our handpairing with *P. g. canadensis* in the lineage leading to the male parent of brood #56. It should be noted however that the "fletcheri" aberration is generally believed to be restricted to the male, and apparently to *P. g. canadensis*. Furthermore, "fletcheri" exhibits significant suffusion of dark scales into both the hindwings and forewings, with an orange smear encroaching ventrally as well as dorsally across the hindwings (see color figure in Scriber and Lintereur, 1983). Our "dark cell" aberration is essentially restricted to the forwings, and only their dorsal surface (Fig. 1).

We do not necessarily mean to imply that the "dark cell" trait (restricted to females) can not be genetically related to the "fletcheri" aberration (apparently restricted to males). In fact, we know that sex-linked (female Y-chromosome) control of the dark morph color polymorphism in *P. glaucus* females (Clarke and Sheppard, 1962) can be transmitted by males in what we consider to have been either a crossover event or a non-disjunction (Scriber and Evans, 1986). The role of *P. g. canadensis* introgression in these events is unclear, but such

gene flow between the two subspecies can be disruptive in a number of ways to other morphological/color traits (Scriber, 1982; Luebke, 1986; Rockey et al, 1987; Scriber, 1987). Unfortunately we will be unable to conduct any further studies of this now extinct "dark cell" lineage.

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Bilateral gynandromorphs, sexual and/or color mosaics in the tiger swallowtail butterfly, *Papilio glaucus* (Lepidoptera: Papilionidae)

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Introduction

Mosaic specimens of Lepidoptera may be of a sexual nature (gynandromorphs or intersexes) or homeotic (involving an inappropriate location for a particular feature or pattern; see reviews by Sibatani, 1980, 1983a, b). Intersexuality typically arises from development errors late in development, and involves an individual which possesses a mosaic of traits, some of which are female, and some of which are male (see McCafferty and Bloodgood, 1986). Gynandromorphs generally develop a sex abnormality much earlier in development; when this occurs at the formation of one of the first two blastomeres, it is possible for individuals to become bilaterally differentiated with one half male and the other half female (Clarke and Ford, 1980; Ayala and Kiger, 1984). The relationship between intersexual mosaics and gynandromorphs is not entirely clear, partly because of the infrequent occurrence of both (Ford, 1955). The combined use of laboratory crosses of species or subspecies, and the recent development of a technique to monitor the heteropyknotic 'Smith' (S) body in the nucleus of somatic cells (derived from the Y-chromosome of female Lepidoptera) should contribute to our understanding of the development of these abnormalities (see Cross and Gill, 1979; Clarke and Ford, 1980, 1983; Bull, 1983).

From the Papilionidae (see Table 1) gynandromorphs have been reported from *Papilio polyxenes asterias* Stoll (Edwards, 1984; Blau, 1978; and Wm. Bergman, pers. comm.); *Ornithoptera victoriae* Gray, and *O. priamus* L., (Schmid, 1973), *O. croesus* Wallace (Parrott and Schmid 1984), *O. poseidon* (D'Abrera 1976); *Parnassius autocrator* (Sbordoni and Forestiero, 1984); *Papilio androgeus* (Sbordoni and Forestiero, 1984) and *Papilio glaucus* L. (Skinner, 1919; Cockayne, 1935; and Clarke and Clarke, 1983). In addition to these published records of gynandromorphs and a large number of additional records reviewed by Cockayne (1935), several hundred sexually mosaic and bilateral gynandromorphic specimens exist in the Lepidoptera collection of James R. Neidhoefer (housed at the Milwaukee Public Museum).

Table 1.   Gynandromorphs (Lepidoptera) reported in the literature.

Family	Genus species	References
Saturniidae	*Automeris io* Fabricius *Eacles imperialis* Drury *Callosamia promethea* (Drury)	Cassino and Reiff, 1917, Hessel, 1964; Muller, 1966; Manley, 1977
Pyralidae	*Hedylepta accepta* (Butter)	Riotte, 1978
Geometridae	*Phaeoura mexicanaria* (Grote) *Antepione thisoaria* (Guenee)	Blanchard, 1969; Durden, 1984
Lymantriidae	*Lymantria dispar* (L.)	Muller, 1976
Nymphalidae	*Limenitis weidemeyerii latisfacia* L. *L. arthemis-lorquini* (Boisduval) *L. arthemis-astyanax* (Fabricius) *Speyeria atlantis dodgei* (Gunder)	Grey, 1959; Perkins and Perkins, 1972; Platt, 1983; H. Romack pers. comm., 1984
Pieridae	*Conepteryx rhamni* L. *G. cleopatra*. L. *Pieris brassicae* L. *P. protodice* Bdv. & LeC *P. rapae* L. *Colias christina* Edwards *C. eurytheme* Bdv. *C. philodice* Godart *Pontia daplidice* (L.) *Tatochila steradice* Stgr.	Emmel, 1964; Hovanitz, 1965; Nekrutenko, 1965; Shapiro, 1970; Gardner, 1972; Sbordoni and Forestiero, 1984; Shapiro, 1978, 1981, and 1985.
Hesperiidae	*Polistes mystic* (Scudder) *P. origines* (Fabr.) *Erynnis horatius* Scudder & Burgess *Hesperia columbia* (Scudder)	Nielsen, 1977; Israel and Cilek, 1982; Scott, 1986
Lycaenidae	*Strymon bazochii* Godart *Lycaena gorgon* (Boisduval) *Agriades rustica rustica (Edwards)* *Mitoura gryneus* (Hubner) *Celastrina ebenina* Clench *Cyaniris semiargus* (Rott.) *C. argiolus* (L.)	Opler, 1966; Riotte, 1978; Rahn, 1982; Sbordoni and Forestiero, 1984; Shuey, 1984; Shuey and Peacock, 1985
Papilionidae	*Papilio polyxenes asterias* Stoll *P. glaucus* L. *P. androgeus* Cramer *Ornithoptera victoriae* *O. croesus* Wallace *O. poseidon* Doubleday *O. priamus* L. *Parnassius autocrator* Avinoff	Skinner, 1919; Schmid, 1973; Cockayne, 1935; Blau, 1978; W. Bergman, pers. comm. 1983; Clarke and Clarke, 1983; Sbordni and Forestiero, 1984; Parrott and Schmid, 1984; D'Abrera, 1976

Table 2.   Progeny (1982 reared) of pairing #9 (*P. g. glaucus yellow morph* female x *P. g. canadensis* male; see text for further details).

Eclosion year	Bilateral Gynandromorph	Males		Females		Dead pupae	Pupae still alive
		eclosed	pharate[1]	eclosed	pharate[1]		
1982	0	7	0	0	0	4	0
1983	1	2*	4	6	1	8	0
1984	0	0	0	6	0	0	0
(Total)	(1)	(9)	(4)	(12)	(1)	(12)	(0)

*One of these males had assymetrical external valuae.
[1]pharate = adults dying inside the pupal case with wings formed.

Table 3. Progeny (1983 reared) of pairing #628 (*P. g. glaucus dark morph* female x *P. g. canadensis* male; see text for further details).

Eclosion year	Bilateral Gynandromorph	Males eclosed	Males pharate[1]	Females eclosed	Females pharate[1]	Dead pupae	Pupae still alive
1983	0	13	0	0	0	9	–
1984	1	25	0	4	0	10	–
1985	0	0	0	13*	0	3	–
(Totals)	(1)	(38)	(0)	(17)	(0)	(22)	(20)

*One of these females is a "yellow intermediate" and one is a "dark intermediate", between the two typical color morphs while all other females are typical yellow morphs (see also Scriber et al, 1987).

The bilateral gynandromorphs in this collection alone include 49 Pieridae, 70 Nymphalidae, 6 Hesperidae, 20 Lycaenidae, 1 Danaidae, and 11 Papilionidae (S. Borkin and A. Young, pers. comm.).

It has been suggested that either viral diseases (Gardiner, 1972; Blau, 1978; Sevastopulo, 1973) or parasitism, and/or abnormal temperatures could be responsible for inducing such abnormalities (Riotte, 1978). It has also been observed that bilateral gynandromorphs and mosaics can occur in multiples from the same brood (Cockayne, 1935; Ford, 1955; Sevastopulo, 1973) and that a variety of laboratory hybrid crosses have yielded intersexual or gynandromorphic individuals (Standfuss, 1900; Whicher, 1915; Cockayne, 1935; Clarke and Sheppard, 1953, 1960; Clarke et al., 1977; Clarke and Ford, 1980; Platt, 1983).

Sir Cyril Clarke and colleagues have been investigating the genetic basis of abnormal wing coloration in *Papilio glaucus* for decades (see Clarke and Clarke, 1983 for a review), and they point out that color mosaics and gynandromorphs are sometimes strikingly visible in *P. glaucus* because of the marked differences between the yellow background of males and yellow morph females and the black/brown background of dark morph females. The Herman Strecker collection (currently on loan from the Chicago Field Museum to the Allyn Museum in Florida) contains a number of such mosaics. This valuable collection, which was assembled during the second half of the 19th century, contains a number of *P. glaucus* mosaics previously described and/or reported upon the literature (e.g. Strecker, 1878; Ehrmann, 1894; Walsten, 1977; Ehle, 1981; Shapiro, 1981b). Edwards (1884) also figures an individual with ½ black and ½ yellow which he describes as a female (Edwards, 1868). Clarke and Clarke (1983) figure similar specimens (essentially half yellow/half dark) from the Strecker collection, one of which is a color mosaic female (from Indiana) and the other an apparent gynandromorph from Pennsylvania.

Partial color (sex?) mosaics in *Papilio glaucus* are also rare, but have been collected in Pennsylvania and previously described by Strecker (1878), and figured by Walsten (1977), Ehle (1981), and Clarke and Clarke (1983). In addition to the partial color mosaics we report here (see also Scriber et al, 1987a), additional cases for *Papilio glaucus* are

known to exist (e.g. personal collections of James Sternberg and David Ritland). The Milwaukee Public Museum contains two partial mosaics of *Papilio glaucus* reared by E. Dluhy in Chicago, Illinois. It is intriguing that the few cases of female coloration patterns unlike their mother's which Clarke and Sheppard (1962; see also Clarke et al., 1976) encountered in their studies were all traceable to a group of pupae obtained from E. Dluhy (from Chicago, Illinois). It was suggested (Scriber et al, 1987a) that similar chromosomally abnormal stock might be involved in both the color mosaics and the abnormal segregation of dark and/or yellow female forms of *Papilio glaucus*. We now feel that an explanation for this abnormality may involve introgression between *P. g. canadensis* and *P. g. glaucus* subspecies near the "blend zone" in Wisconsin (Scriber 1982, 1983) and across the Great Lakes region (Scriber et al., 1987b). In this paper we shall report aspects of our laboratory studies with members of the North American tiger swallowtail, *Papilio glaucus* L., group.

Methods

In the past 6 years we have reared through to the adult stage or collected in the field (from southern Florida to northern Canada) over 28,000 specimens of the *Papilio glaucus* species complex. Field captured specimens have included all three *P. glaucus* subspecies as well as *P. eurymedon, P. rutulus, P. multicaudatus*, and *P. alexiares garcia*. Lab reared specimens have included pure stock of all of these species and subspecies as well as geographic site crosses within subspecies, subspecies-level and species-level crosses.

Oviposition by adult females is induced by placing each wild-captured or hand-paired female into its own clear plastic box (approximately 10 cm deep × 15 cm × 30 cm) with a moist paper towel and selected larval foodplant leaves. Leaf turgor was maintained in these plants by use of floral aquapics® (water-filled plastic vials with a rubber cap, through which leaf petioles or small branches can be inserted; see Scriber, 1977). Heat and light were provided by incandescent bulbs placed at a distance of approximately 0.3-0.5 meter from the plastic boxes.

Larvae were reared to pupation on one of various foodplants, (leaves were changed three times per week) under controlled environment conditions (16:8 photo-scoto-phase with corresponding temperatures of 23°/19°C, respectively). Pupae were weighed 2 days after pupation (the weight subsequently serving an identification number for the individual) and then placed in individual cylindrical screen cages (15 cm diameter × 12 cm height) under larval rearing conditions or similar laboratory conditions (21-24°C) to permit development and eclosion as adults. Direct developing individuals normally emerged within 2-3 weeks after pupation. Other pupae were given at least 6 weeks before being refrigerated in darkness (at 40-45°F for 3 months or more) to break diapause. Hand-pairings were generally attempted 12-48 hrs after adult female eclosion and 2-3 days after male eclosion. Since dark female color suppression and obligate diapause are linked on the X-chromosome (R. Hagen and J.M. Scriber, manuscript), we observe one year delayed emergence of F, females from both yellow (Table 1) and dark (Table 2) females when maled with *P.g. conadensis* males.

Table 4. Gynandromorphs, mosaics, and their siblings (1981-1986).[a,m]

						Siblings in the Brood			
Brood #	Rearing Year	Gynand.	Mosaics	Fig. #	Males	Yel	Dk	Pupae (as of 7 Nov. 86)	Dead Pupae
9	82	1		1	13[b]	13	0	0	12
628	83	1		2	38	17[c]	0	20[d]	22
631	83	1		10	6	6	0	2	3
1091	84	1		4	2	0	1	0	0
2025	84	1		9	1	2	0	0	0
2830	85	1		7	40	0	0	22	3
3622[e]	86	1		6	8	0	18	9	0
3935	86	1		8	6	0	11	13	0
4196[e]	86	1		5	26	1	10	20	0
4210	86	1		3	31	2	27	4	3
JMS	81		1	11	5	0	12[n]	0	0
658	83		1	14	7	0	10	1	0
688	83		14	20	22[f]	0	24[g]	34[h]	6
717	83		1	29	30	0	34	0	1
1064	84		1	12	9	0	11	0	1
1128	84		1	15	16	0	24[i]	0	1
1348	84		1	28	22	18[j]	0	2	0
1351	84		1	27	52	37[j,k]	1	24	7
1534	84		1	26	0	0	0	0	0
1905	84		1	X	23	0	31	3	7
1914	84		1	23	42	0	41	14	2
1999	84		1	13	9	0	6	0	1
2030	84		1	X	7	0	2	0	0
3122	85		1	X	1	0	0	0	0
3604	86		1	24	11	0	15	18	0
3770	86		1	25	34	0	3[l]	28	0
3800	86		1	17	29	0	28	19	1
3973	86		1	16	19	0	15	6	0
4230	86		1	30	8	2	8	1	0
Subtotals:		10	32		512	98	320	240	70
Total Reared to pupae = 1282									

[a]Pharate adults are included with "emerged adults".

[b]One male has asymmetrical valvae.

[c]One female is a "yellow intermediate" and one is a "dark intermediate".

[d]Two of these pupae are unaccounted for as of 1984.

[e]An additional emerged adult has no sex recorded on printout.

[f]One male has very reduced claspers and one male has extra dark scaling.

[g]Two females are slight intermediates and one female has extra yellow and unusually high density blue.

[h]Approximately 6 weeks after pupation, these were refrigerated to break diapause and not brought out of the refrigerator the first time until 14 mos. later. Although they still appear viable, it is uncertain if they will eclose in the future.

[i]One female is a dark intermediate.

[j]Some of these may be "yellow intermediates" but did not get recorded as such. They are not all pinned now and colors cannot be easily verified.

[k]Four females are "yellow intermediates" (i.e., more yellow than dark).

[l]Two females are "dark intermediates" (i.e., more dark than yellow).

[m]Wild collected mosaics (see Table 3) are excluded from this table as they have no sibling data.

[n]Two females were "dark intermediates".

Table 5.   Phenotype, geographic origin, and brood number of gynan-
           dromorphs.

Phenotypes &/or geographic origins[a]	Gynandromorphs		
	Perfect Bilateral	< 50% one sex	Brood # b generating aberrant
Georgia		1	2025
Ohio		3	631
			3622
			3935
Texas		1	1091
Pa Yel x Pgc (Juneau)	1		9
S. Car Dk x Pgc (Marinette)	1		628
Ill. Dk x F$_1$ (GaDk x Pgc)		1	4196
W. Va. Dk x *P. rutulus*		1	2830
Ohio Dk x *P. alexiares*	1		4210
Totals	3	7	

[a]When phenotype or geographic site crosses are listed, the female
background is listed first.
[b]For information on siblings of aberrants, look up brood numbers on
table #1.

Results

Of the 28,000 reared adults we have observed 10 gynandromorphs
and 32 color mosaics (Tables 4 and 5). Of the obvious gynandromorphs
four of the five perfect or near perfect bilateral gynandromorphs (Figs.
1-5) were progeny of subspecies of species crosses. The fifth could also be
considered a subspecies cross if the Texas population is *P. g. australis*
(Scriber, 1986). Of the remaining five gynandromorphs (Figs. 6-10) only
one (Fig. 7) involves two different taxa. Of approximately 8,500 field
collected specimens during 1981-1986, we have never collected an
obvious gynandromorph.

Of the 32 color mosaics listed in Table 4, all but 6 are of either pure *P.
glaucus glaucus* or *P. g. australis* (Table 6). These mosaics are dark
morph females with varying amounts of yellow dorsally and/or ven-
trally on their wings or body. Of the 37 total *P. glaucus* mosaics, one was
a field collected *P. g. australis* from Highland Co., Florida (Fig. 22) and
two were field collected *P. g. glaucus* from Dane Co., Wisconsin (Figs. 18

Table 6.   Phenotype, geographic origin, and brood number of color mosaics.

Phenotypes &/or geographic origins[a]	Gynandromorphs		Brood # [b] generating aberrant
	Dk w/ exceptional color yellow	Yel w/ exceptional color black	
Georgia	3		1064
			2030
			3122
Illinois	2		1905
			1999
Ohio	4		658
			1128
			3800
			3973
Texas	2		1039 (wild)
			3270 (wild)
Wisconsin	17[c]		JMS
			688
			729 (wild)
			736 (wild)
Georgia x Ohio	1		3604
(Ga. x Wis.) x Ill.	1		1914
P. glaucus australis	1		no # (wild)
Ga. Dk x Pgc (Green Lake)		1	1348
Ga. DK x Pgc (Tompkins)	1[e]		3770
Tx Dk x Pgc (Juneau)		1	1534
Tx Dk x Pgc (Wood)		1	1351
B_1 (F_1 (GaDk x Pgc) x Wis.) x Pga	1		717
Ill Dk x *P. alexiares*	1		4230
Totals	34[f]	3	

[a]When phenotype or geographic site crosses are listed, the female background is listed first.

[b]For information on siblings of aberrants, look up brood numbers on table #1.

[c]Of these 17 mosaics, 14 were siblings in brood #688.

[d]Counties of specimen origin are shown in parentheses and all are Wisconsin except Tompkins which is New York.

[e]This is actually an intermediately colored specimen but the exceptional color is yellow.

[f]Of the 34 dominantly dark color mosaics listed, 27 are shown in the following illustrations. (All other aberrants in this table are illustrated).

Fig. 1.   A bilateral gynandromorph (from brood #9, pupal wt. 1.0605, ex ova, reared in 1982, eclosed on 21 May 1983) from a lab cross of a yellow morph *P. g. glaucus* female (2nd generation lab-reared from wild stock collected by W. Houtz in Schuylkill Co., Pennsylvania) mated to a wild collected male *P. g. canadensis* from Juneau Co. Wisconsin. A) dorsal, B) ventral.

Fig. 2.   A bilateral gynandromorph (from brood #628, pupal wt. 0.9310, ex. ova, reared in 1983, eclosed on 30 May 1984) from a lab cross of a dark morph *P. g. glaucus* female (reared from eggs obtained from a wild dark morph female collected by R. Peigler in Pickens Co., South Carolina) mated to wild collected male *P. g. canadensis* from Marinette Co., Wisconsin (collected 1-5 July 1983 by Don Caine). A) dorsal, B) ventral.

Fig. 3.   A bilateral gynandromorph (from brood #4210, pupal wt. 1.1099, ex. ova reared in 1986, eclosed on 26 Sept. 1986) from a lab cross of a dark morph *P. g. glaucus* female (2nd generation lab reared from wild stock collected by J. Thorne and MHE in July 1985 in Adams Co., Ohio) mated to a wild collected male *P. alexiares garcia* from Nuevo Leon, Mexico (collected 2, 3 Aug. 1986 by W. Warfield, D. Robacker and MHE). A) dorsal, B) ventral.

Fig. 4.   A nearly perfect bilateral gynandromorph, or sexual mosaic, (from brood #1091, pupal wt. 1.1493, ex. ova, reared in 1984, eclosed on 27 June 1984) from a wild collected dark morph *P. g. glaucus* female from Jasper Co., Texas (collected on 9 April 1984 by JMS and MHE). A) dorsal, B) ventral.

Fig. 5.   A gynandromorph, or sexual mosaic, which appears to be more than 50% female (from brood #4196, pupal wt. 1.2779, ex. ova, reared in 1986, eclosed on 29 Sept. 1986) from a lab cross of a dark morph *P. g. glaucus* female (reared from eggs obtained from a wild dark morph female collected by M. Berenbaum in Champaign Co., Illinois in June 1986) mated to a subspecies hybrid male (whose mother was the daughter of a dark morph *P. g. glaucus* female collected in Georgia in Aug. 1985 by J. Maudsley and whose father was a P. g. canadensis collected in Lincoln Co., Wisconsin on 3 June 1986 by D. Ware, V. Viegut and MHE). A) dorsal, B) ventral.

Fig. 6.   A gynandromorph, or sexual mosaic, which appears to be more than 60% female (from brood #3622, pupal wt. 1.2866, ex. ova, reared in 1986, eclosed on 12 Aug. 1986) from a pure *P. g. glaucus* lineage (in which the mother was the daughter of a dark morph female collected in May 1986 in Hocking Co., Ohio by S. Stribling and the father was the son of a dark morph female collected in July 1985 in Adams Co., Ohio by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 7.   A gynandromorph, or sexual mosaic, which appears to be more than 60% male (from brood #2830, pupal wt. 1.1341, ex. ova, reared in 1985, eclosed on 1 June 1986) from a dark morph *P. g. glaucus* female (reared from eggs obtained from a dark morph female wild collected in Clay Co., W. Virginia on 12 July 1984 by W. Warfield and MHE) mated to a wild collected *P. rutulus* male (reared from eggs obtained from a wild female collected by R. Dowell in Sacramento Co., CA). A) dorsal, B) ventral.

Fig. 8.   A gynandromorph, or sexual mosaic, which appears to be more than 75% female but with male claspers (from brood #3935, pupal wt. 1.5321, ex. ova, reared in 1986, eclosed 14 Sept. 1986) from a wild collected dark morph *P. g. glaucus* female (collected in Scioto Co., Ohio on 4 July 1986 by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 9.   A gynandromorph which appears to be more than 80% male (from brood #2025, pupal wt. 1.1541, ex. ova, reared in 1984, eclosed on 12 May 1985) from a yellow morph *P. g. glaucus* female wild collected in Clarke Co., Georgia (collected on 29 Aug. 1984 by J. Maudsley). A) dorsal, B) ventral.

Fig. 10.   A gynandromorph which appears to be more than 90% male (from brood #631, pupal wt. 0.9980, ex. ova, reared in 1983, eclosed on 25 Oct. 1984, was paired to 2054 but produced no progeny) from a yellow morph *P. g. glaucus* female wild collected in Adams Co., Ohio (collected on 9 July 1983 by W. Warfield and

MHE). A) dorsal, B) ventral.

Fig. 11.   A female color mosaic (ex. ova, reared in 1981 by D. Ritland and J. M. S., eclosed Aug. 1981) from a normal appearing dark morph *P. g. glaucus* female (collected in Dane Co., Wisconsin in June 1981 by P. Kingsley and D. Ritland). A) dorsal, B) ventral.

Fig. 12.   A female color mosaic (from brood#1064, pupal wt. 1.2526, ex. ova, reared in 1984, eclosed on 9 July 1984) from a wild dark morph *P. g. glaucus* female (collected in Oglethorpe Co., Georgia on 14 Apr. 1984 by J. Maudsley). A) dorsal, B) ventral.

Fig. 13.   A female color mosaic (from brood #1999, pupal wt. 1.2960, ex. ova, reared in 1984, eclosed on 10 May 1985) from a wild dark morph *P. g. glaucus* female (collected in Rock Island Co., Illinois on 25 Aug. 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 14.   A female color mosaic (from brood #658, pupal wt. 0.9439, ex. ova, reared in 1983, eclosed 2 June 1984) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 9 July 1983 by W. Warfield and MHE). A) dorsal, B) ventral.

Fig. 15.   A female color mosaic (from brood #1128, pupal wt. 1.5200, ex. ova, reared in 1984, eclosed 12 July 1984) from lab paired parents which were propgeny of two wild dark morph *P. g. glaucus* females (both collected in Adams Co., Ohio and 9 July 1983 by W. Warfield and MHE). A) dorsal, B) ventral.

Fig. 16.   A female color mosaic (from brood #3973, pupal wt. 1.1323, ex. ova, reared in 1986, eclosed 18 Sept., 1986) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 5 July 1986 by J. Thorne and MHE). A) dorsal, B) ventral.

Fig. 17.   A female color mosaic (from brood #3800, pupal wt. 1.4466, ex. ova, reared in 1986, eclosed 7 Oct. 1986) from a wild dark morph *P. g. glaucus* female (collected in Adams Co., Ohio on 6 July 1986 by J. Thorne, and MHE). A) dorsal, B) ventral.

Fig. 18.   A wild collected *P. g. glaucus* female color mosaic (assigned #729 and set up for oviposition but died laying only one infertile egg: collected in Dane Co., Wisconsin on 7 Aug. 1983 by MHE). A) dorsal, B) ventral.

Fig. 19.   A wild collected *P. g. glaucus* female color mosaic (assigned #736 and set up for oviposition but died laying no eggs: collected in Dane Co., Wisconsin on 7 Aug. 1983 by W. Warfield). A) dorsal, B) ventral.

Fig. 20.   Fourteen female siblings with various color mosaic patterns were generated from one brood (#688, ex. ova, reared in 1983) from a normal appearing wild dark morph *P. g. glaucus* female (collected in Dane Co., Wisconsin on 1 Aug. 1983 by W. Warfield). Nine of those female siblings are shown here. A) dorsal, B) ventral.

A)	Pupal wt.	1.2253 g;	eclosed	25 Oct.	1984
B)	" wt.	0.9834 g;	"	29 May	"
C)	" wt.	1.1072 g;	"	30 May	"
D)	" wt.	1.2296 g;	"	25 Oct.	"
E)	" wt.	1.1742 g;	"	25 Oct.	"
F)	" wt.	1.3444 g;	"	1 June	"
G)	" wt.	1.2375 g;	"	25 Oct.	"
H)	" wt.	1.2555 g;	"	25 Oct.	"
I)	" wt.	0.9885 g;	"	31 May	"

Fig. 21.   A wild collected *P. g. glaucus* female color mosaic (assigned #1039 and set up for oviposition: she laid 5 eggs which produced 2 larvae. One reached the adult stage as a normal appearing male which was not mated.) wild collected (in Jasper Co., Texas in April 1984 by JMS and MHE). A) dorsal, B) ventral.

Fig. 22.   A wild collected *P. g. australis* female color mosaic (collected in Highlands Co., Florida in Apr. 1981 by B. Giebink, JMS and MHE). A) dorsal, B) ventral.

Fig. 23.   A female color mosaic (from brood #1914, pupal wt. 0.9309, ex. ova,

reared in 1984, eclosed 28 Oct. 1984) from a dark morph. *P. g. glaucus* female (the daughter of a lab pairing of a dark morph *P. g. glaucus* female reared from stock collected in Oglethorpe Co., Georgia in April 1984 by J. Maudsley, mated to a wild *P. g. glaucus* male collected in Richland Co., Wisconsin on 7 June 1984 by S. Sippl, and JMS) lab mated to a wild *P. g. glaucus* male (collected in Rock Island Co., Illinois on 11 Aug. 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 24.   A female color mosaic (from brood #3604, pupal wt. 1.4616, ex. ova, reared in 1986, eclosed 4 Aug. 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #3145 collected in Habersham Co., Georgia in Aug. 1985 by J. Maudsley) lab mated to a *P. g. glaucus* male (the son of a wild dark morph *P. g. glaucus* female, #2868, collected in Adams Co., Ohio on 9 July 1985 by J. Thorne and MHE).

Fig. 25.   A female color mosaic (from brood #3770, pupal wt. 1.7029, ex. ova, reared in 1986, eclosed 25 Aug. 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #3104, collected in Athens Co., Georgia in Aug. 1985 by Λ) lab mated to a wild *P. g. canadensis* male (collected in Tompkins Co., N.Y. by R. Lederhouse on 17 June 1986). A) dorsal, B) ventral.

Fig. 26.   A female color mosaic (from brood #1534, pupal wt. 13389, ex. ova, reared in 1984, eclosed 3 Aug. 1985) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #1038, collected in Jasper Co., Texas on 9 April 1984 by JMS and MHE) lab mated to a wild *P. g. canadensis* male (collected in Juneau Co., Wisconsin on 18 June 1984 by W. Warfield). A) dorsal, B) ventral.

Fig. 27.   A female color mosaic (from brood #1351, pupal wt. 1.2429, ex. ova, reared in 1984, eclosed 14 May 1985) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female, #1025, collected in Newton Co., Texas in April 1984 by JMS and MHE) lab mated to a wild *P. g. canadensis* male (collected in Wood Co., Wisconsin on 12 June 1984 by C. Plazk, Y. Allen, K. Hale, and W. Warfield). A) dorsal, B) ventral.

Fig. 28.   A femal color mosaic (from brood #1348, pupal wt. 1.1453, ex. ova, reared in 1984, eclosed 1 July 1986) from a dark morph *P. g. glaucus* female (the daughter of a wild dark morph *P. g. glaucus* female with yellow discal cells, #1231, collected in Oglethorpe Co., Georgia in May 1984 by J. Maudsley) lab mated to a wild *P. g. canadensis* male (collected in Green Lake Co., Wisconsin on 12 June 1984 by J. Thorne, S. Sippl, and MHE). A) dorsal, B) ventral.

Fig. 29.   A female color mosaic (from brood #717, pupal wt. 1.3006, ex. ova, reared in 1983, eclosed 26 Sept. 1983) from a "peppered"-colored yellow female (from brood #558; a dark morph female GA Pgg x Pgc, backcrossed to a Pgg from Wisc.) mated to a wild *P. g. australis* male (collected in Highlands Co., Florida on 3 Aug. 1983 by JMS). A) dorsal, B) ventral.

Fig. 30.   A female color mosaic (from brood #4230, pupal wt. 1.0948, ex. ova, reared in 1986, eclosed 4 Oct. 1986) from a dark morph *P. g. glaucus* female (the daughter of a dark morph *P. g. glaucus* female, #3540, wild collected in Champaign Co., Illinois in June 1986 by M. Berenbaum) lab mated to a wild *P. alexiares* male (collected in Nuevo Leon, Mexico 2-3 Aug. 1986 by W. Warfield, D. Robacker, and MHE). A) dorsal, B) ventral.

and 19). Fourteen other *P. g. glaucus* mosaics are all siblings from one wild collected female from Dane Co., Wisconsin (e.g., Fig. 20). Two field captured females from Texas were mosaics (Table 6; Fig. 21).

Of the six lab-reared mosaics that were not of "pure" subspecies lineage four are progeny of subspecies crosses between *P. g. glaucus* females and *P. g. canadensis* males (Table 6). Three of these are yellow females with the exceptional and asymmetrical color being black (Figs. 26-28) while the fourth is an intermediately colored female with the exceptional color being yellow (Fig. 25). The fifth non-pure *P. g. glaucus* mosaic is the product of a lab pairing involving all three *P. glaucus* subspecies as ancestors. The mosaic is 50% *P. g. australis*, 12.5% *P. g. canadensis*, and 37.5% *P. g. glaucus* (Fig. 29). A sixth mosaic arose from a *P. g. glaucus* paired with a male *P. alexiares garcia* (Fig. 30).

Discussion

The reported frequency of color mosaics or gynandromorphs is quite low. We have reared more than 28,000 individuals of the *Papilio glaucus* complex (1981-1986) and have observed only 37 color mosaics and only 5 perfect or nearly perfect bilateral gynandromorphs. While from previous literature records it would seem that the "blend zone" (i.e. the zone of potential/probable hybridization) across the Great Lakes and Appalachian Mountain region has accounted for most previously reported aberrant types of *P. glaucus* (Edwards, 1868, 1884; Skinner and Aaron, 1888; Ehrman, 1893; Howard, 1899; Clark and Clark, 1951; Ehle, 1981; Scriber et al, 1985; H. Romack, pers. comm.), we have in this 5-year period observed mosaics in stock from Georgia, Texas, Illinois and Ohio as well as Wisconsin. In addition to our Dane County field-captured mosaics (near the zone of suspected hybridization), color mosaics exist from Richmond County, NY (5 July 1971; A.M. Shapiro; currently in the Univeristy of California-Davis Collection) and Washington County, PA (9 May 1927; George F. Patterson Collection at Pennsylvania State University), both also near the proposed blend zone (see Ritland and Scriber, 1985; Scriber and Hainze, 1987).

Since in our studies, 4 of 5 perfect or nearly perfect bilateral gynandromorphs are progeny of subspecies or species crosses in the *P. glaucus* species complex, and since 32 of 37 mosaics are progency of "pure" (i.e. single subspecies) lines, it could be argued that factors inducing the expression of gynandromorphic traits are likely to be different than factors inducing the expression of mosaic traits. In fact, for the occurence of mosaics the observed distribution between inter-taxa versus intra-taxa crosses does not differ from the expected (n = 5105, Chi square, p = 0.25), whereas for the near perfect bilateral gynandromorphs significantly more resulted from the inter-taxa crosses (n = 11, 112, Fisher Exact test, p < 0.038).

The mechanism(s) by which hybridization may catalyze these events leading to color/sexual abnormalities is uncertain at this time. Clarke

and Clarke (1983; see also Scott, 1986) suggest that in *P. glaucus* maleness is dependent upon the presence of two X chromosomes and femaleness is dependent upon a single X chromosome (the Y chromosome assumed to be relatively inert, except of course that it carries the locus for dark morph color; Clarke and Sheppard, 1962; Clarke et al., 1976). If this is true (cf. Tazima, 1964; where femaleness in silk moths may be related to the Y chromosome), then the *P. glaucus* sexual mosaics in the Strecker collection may represent the results of either non-disjunction or double fertilization (Clarke and Clarke, 1983). Three specimens are figured by Clarke and Clarke: 1) The female half black/half yellow may be the result of non-disjunction, i.e. XY/XO with the gene for melanism on the Y and the XO half being yellow; 2) the gynandromorph which is approximately half black (female) and half yellow (male) may be the result of a double fertilization (i.e. XX/XY); and 3) a sexual mosaic specimen (a partial mosaic described by Howard, 1899) could be the result of XX/XY (non-disjunction) or XY/XO (double fertilization). While Clarke and Clarke were not aware of the potential hybridization of *P. g. glaucus* with *P. g. canadensis*, we now suggest with our laboratory results that hybrid individuals in the "blend zone" may indeed be naturally predisposed to non-disjunction or chromosome loss as appears to be the case with other *Papilio* hybrids (see Clarke et al., 1977). In fact, we also have evidence suggesting the loss of a segment of the Y-chromosome controlling the melanic (dark) background coloration in brood number 674 reared in 1983 (with transfer of this chromosome fragment independently, via a crossover or via a non-disjunction) with the melanic locus to at least one of the male sibs!). This aberrant male, when mated to a virgin *P. g. canadensis* from northern Wisconsin and to a yellow morph *P. g. glaucus* female from a yellow morph lineage from Ohio, produced daughter progeny which were both typical dark morph and typical yellow morph (Scriber et al., 1987). Never before has any male *P. glaucus* been known to transmit the trait for female melanism (see Scriber and Evans, 1986).

The ability to distinguish between color mosaics and sexual mosaics is not easy, even with the distinctive pattern of the melanic form female. It is even more difficult to distinguish between yellow morph gynandromorphs (where the male and female regions differ from each other both phenotypically and in genetic constitution) and intersexes (where male and female regions appear phenotypically different, but have identical chromosomal constitution: see Whiting et al., 1934; Doutt and Smith, 1950; Clarke and Ford, 1980). We hope that additional studies will clarify the genetic basis of gynandromorph production (see reviews by Cockayne, 1935; Drescher and Rothenbuhler, 1963), and of the differential suppression (modification) of female phenotypes dark/yellow polymorphism in *Papilio glaucus* due to hybridization. Some morphological characteristics differ between the male and female halves of the F_1 specimens figured (Fig. 1 and Fig. 2) as well as the obvious differences in melanism in Fig. 3. The usefulness of developmental physiology

studies in this regard would be significant, especially since the color patterns on the upper and lower surfaces of Lepidoptera wings develop independently (see Nijhout, 1981 for a discussion), and can be modified by environmental temperature (Ritland, 1983).

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Oviposition on Peripheral Hosts by Dispersing *Pieris napi* (L.) (Pieridae)

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Abstract. Females of *Pieris napi* dispersing through an unfavourable habitat were able to detect *Cardamine flexuosa L.* individuals hidden from sight. Such peripheral hostplants receive more *P. napi* eggs than conspecifics at the population centre; this is partly due to females laying several eggs at a single visit, apparently a tactic adopted in response to low hostplant density. Inverse density-dependent host selection may have important effects on hostplant communities, such as increased herbivore pressure on peripheral host species.

Introduction

Several recent investigations have reported that individuals within a butterfly population may adopt different reproductive tactics in response to environmental variation (Wiklund, 1981; Tabashnik et al., 1981). For instance, females experiencing low availability of foodplants may respond by ovipositing more readily upon suboptimal hosts (Singer, 1982, 1984) or by increasing the number of eggs deposited on a host (Parker and Courtney, 1984). Further observations are badly needed to document the factors which influence such changes in behaviour. However, it is normally hard to make extensive observations on females in marginal habitats, where the insects are, by definition, scarce. I report here observations on *Pieris napi* (L.) at Delamere Forest, Cheshire, England, where individual females were regularly watched during July and August 1982, as they entered apparently unfavourable habitats during dispersal from population centers. Several unusual behaviours were seen, and are described here because of their importance to population and community processes.

Observations and Results

Two population centres for *C. flexuosa* were found in wet meadows to the north-east of Delamere. *Nasturtium officinale* R. B and *Cardamine pratensis* L. (both Cruciferae) were the predominant hostplants, with some *C. flexuosa*. Both populations bordered a large coniferous plantation which contained felled areas where Bracken (*Pteridium aquilinum* L.) and Bramble (*Rubus fructicosus* L. agg.) grew densely. 600 m of trees separated the two marshy areas where, in July-August, the second brood of *P. napi* was in good numbers, making short flights among the

Table 1.   Individuals of *P. napi* observed in two areas of Delamere Forest on
           28.7. and 4.8.1982. Comparison of the main population (marsh) with
           dispersing individuals (heath) yields a significant difference in
           sex-ratio ($X^2 = 5.906$ $p < 0.025$).

P. napi		*Marsh*	*Heath*
	Males	32	17
	Females	8	15

vegetation. A few butterflies were also seen in the felled areas of the
plantation, flying rapidly and directly across the apparently unsuitable
habitat. The sex ratios of individuals in the marsh and heathland areas
were significantly different: proportionately more females were seen
away from the main population areas (Table 1). This difference probably
arises more from differential conspicuousness of the two sexes in the
main population areas (Gilbert and Singer, 1975) than from differential
dispersal of the sexes (e.g., Shapiro, 1970). No differences were found in
spermatophore counts of five females from either habitat; all females
had mated once.

On 28th July, two females were observed in the felled area in
characteristic "oviposition search" style of flight, which is adopted in the
vicinity of hostplants (Chew, 1975; Wiklund and Ahrberg, 1978). Close
inspection showed that these females had located a small group of *C.
flexuosa* plants, growing in an old, moist ditch underneath the Bracken.
These hostplants were located 900 m away from each of the two marshy
areas. The hostplants were largely hidden from sight below the Bracken,
and subsequent observation on other *P. napi* individuals confirmed that
females did not visually detect the *C. flexuosa* patch. Butterflies were, on
several occasions, seen to switch, from rapid, direct flight to slow,
host-location flight, when in the vicinity of completely hidden *C. flex-
uosa*. Olfactory stimulation of searching behaviour of Pierinae has long
been suspected; antennal chemoreceptors are known to respond to
glucosinolates, a major family of phytochemicals in Cruciferae (Den
Otter et al., 1980). Field observations of such behaviour have been
lacking until now. No females were observed to search in any other felled
or wooded area, and an extensive search revealed only two more *C.
flexuosa* plants in the wood; one plant bore four *P. napi* eggs.

On adopting the 'oviposition search' mode of flight, the female would
investigate the ground layer of vegetation, approaching and occasionally
landing upon small herbs. Females were sometimes seen deep under-
neath the Bracken, flying among the fronds in their search for hosts. On
locating a host, a female would flutter around it, settle on a leaf and,
bending the abdomen underneath, deposit an egg. On two occasions (of
32 observed ovipositions) a second egg was immediately deposited. On
five other occasions the female flew up and returned to the same plant to
lay a second egg. Multiple oviposition by *Pieris rapae* L is well known,
but *P. napi* has rarely been seen to lay more than one egg at a host (F.S.
Chew, pers. comm.). In this sub-population of dispersing individuals,

Table 2.   Average height (cm.) and leaflet number (with standard error) of *C. flexuosa* individuals growing in four categories of shading by Bracken, with the average eggload of *P. napi* on such plants (Number of eggs/Number of leaflets). Data from the marsh population are given for comparison. All data collected 28.7. 1982.

	Shading	n	Height	Leaflets	Eggload
Heath	<25%	7	9.3	5.29(1.82)	1.16
	25–50%	15	9.0	3.87(1.10)	1.12
	51–75%	14	15.0	4.86(0.90)	0.32
	>75%	26	18.1	11.69(2.61)	0.27
Marsh		35	14.1	9.20(1.31)	0.12

multiple oviposition seemed frequent, though it was never seen in the main marshy populations.

Numerous eggs were found on the 62 *C. flexuosa* individuals in the ditch. Table 2 presents these data for four groupings of plants according to the degree of overtopping by Bracken. Seven individuals had less than 25% of the sky above obscured by Bracken (estimated by eye); these plants received a very heavy load of *P. napi* eggs, with over one egg per leaflet (far more than could be supported through larval development). The majority of *C. flexuosa* were more shaded and 21 (41.9%) were almost completely obscured by Bracken. Relatively few eggs were found on heavily shaded plants, although these were the largest. Chew (1977) reports that shaded individuals of Nearctic *Cardamine* similarly escape *P. napi* oviposition. These and similar results in *Anthocharis cardamines* L. have been interpreted as consequences of females restricting their activity to areas of direct sunshine (Courtney, 1982). Note that the eggloads, of even the heavily shaded *C. flexuosa* plants in the ditch, are much heavier than those seen in the marshes where *C. flexuosa* was more plentiful. Figure 1 illustrates the combined effects of shading levels, and of host size, which also influences eggload. Similar results obtain in Nearctic *P. napi* and *Cardamine* populations (F. S. Chew, pers. comm.). Since a single *P. napi* larva would consume all the above ground biomass of a *C. flexuosa* plant, probably few hosts in the ditch escape serious grazing.

Examination of the number of eggs on the leaflets of those plants with at least one egg suggests a tendency towards clumped distributions (Table 3). The trend occurs in all three shading classes, but is significant only in the most heavily shaded class. The results contrast with data from the marsh sub-population where the distribution fortuitously agrees well with the random expectation. These results are to be expected if multiple oviposition occurs in the ditch, but not in the marsh.

Discussion

The very large eggloads, received by some *C. flexuosa* plants in the ditch, are far in excess of the number which can be supported through larval development. Courtney and Courtney (1982) described similar
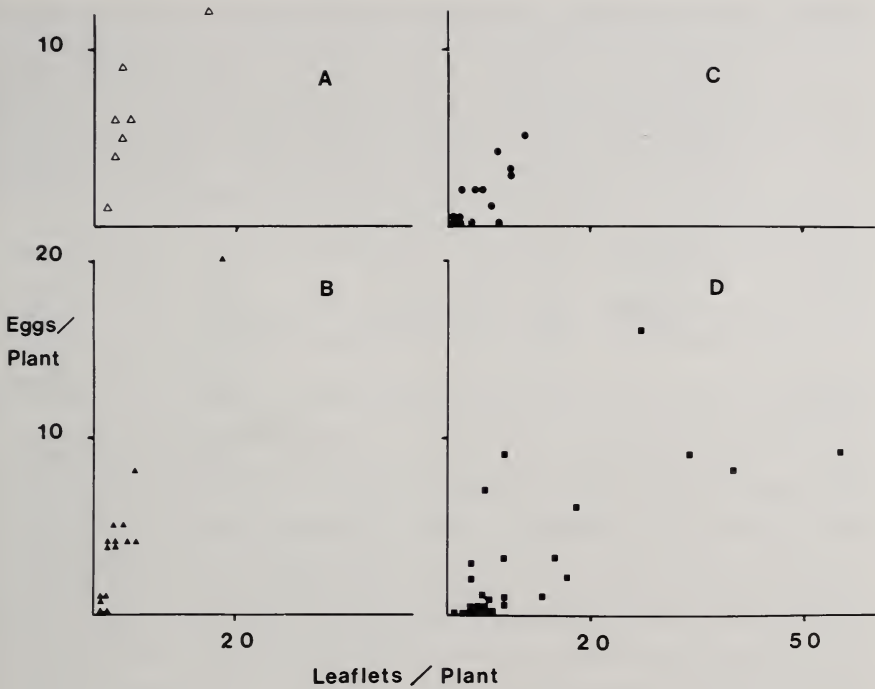
Fig. 1. The relationship between the number of leaflets on *C. flexuosa* individuals and the number of *P. napi* eggs deposited, in four categories of shading (determined by eye). The value of the correlation coefficient, r, is shown

A. (<25% of Sky obscured)   r = .810   p < 0.005
B. (25–50%)   r = .955   p < 0.001
C. (51–75%)   r = .779   p < 0.001
D. (>75%)   r = .698   p < 0.001
All data summed   r = .555   p < 0.001

inverse density dependent egg distributions in *P. napi* and *A. cardamines* and ascribed them to changes in receptivity of females. It is suggested that females accept suboptimal oviposition sites (such as those already bearing an egg or larva) when hosts are rare. The present results, which link increased eggloads to observed changes in behaviour, support the idea that females modify their behaviour in response to resource availability.

Such behaviour may have important consequences for population and community processes: Shapiro (1975) and Courtney and Courtney (1982) show how both intra- and inter-specific competition are greatly increased by clumped egg distributions. The present study suggests that such competition may be more important in peripheral habitats and in the offspring of dispersing individuals, than in main population centers. Similarly, Wiklund and Ahrberg (1978) have discussed the

Table 3. Distributions of *P. napi* eggs over leaflets of those *C. flexuosa* plants with eggs (elimination of other plants from the analysis follows the conservative procedure of assuming that such individuals were unsuitable/unavailable for oviposition). Only three classes of shaded plant are given for the heathland site, the two lighter classes (<25% and 25−50%) being summed (mean eggloads are very similar as in Table 2). Values are given for X^2 comparisons with expected values from a random (Poisson) distribution.

		Eggs per leaflet									
	Shading	0	1	2	3	4	5	9	X^2	d.f.	p
Heath	<50%	35	28	17	8	3	2	—	3.13	3	n.s.
	51−75%	40	10	2	1	—	1	—	1.94	2	n.s.
	>75%	231	22	9	5	2	2	1	36.90	2	<0.001
Marsh		69	17	2	—	—	—	—	0.03	2	>0.975

effect of inversely density related oviposition in a community of host-plant species which differ in their dispersion. *A. cardamines* attack was most severe on low density or highly dispersed hosts. In the present study, *P. napi* in the marsh were mainly supported by the hosts *C. pratensis* and *N. officinale*. *C. flexuosa* individuals in the marsh suffered fewer attacks than conspecifics growing alone in the ditch. It seems that the *C. flexuosa* population in the wood suffers from being in the vicinity of large marshland populations of other Cruciferae. It is a general prediction from the studies of Wiklund and Ahrberg, and of Courtney and Courtney, that peripheral species surrounding major hostplant localities may suffer disproportionately from herbivore attack.

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Enzyme electrophoresis and interspecific hybridization in Pieridae (Lepidoptera)-The case for enzyme electrophoresis

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Abstract. In a comparison of results from laboratory intertaxa hybridizations and enzyme electrophoresis in Pieridae, Lorkovic (1986) recognizes differences in the estimates of genetic relationships of the taxa investigated. Lorkovic concludes in his paper that these differences are due to the electrophoretic approach. It is the purpose of this publication i) to analyze this opinion, ii) to discuss possible limitations and pitfalls of the hybridization approach, and iii) to show that an adequate interpretation of the data may well lead to a generally accepted idea on the genetic relationships in Pieridae.

Introduction

In a recent paper, Lorkovic (1986) compared results from his impressive work on artificial interspecific hybridization in Pieridae with results of an analysis of the genetic relationships in this family by means of enzyme electrophoresis. Lorkovic (l.c.) concludes that the observed discrepancies between the results of the two approaches are due to the electrophoretic analysis which gives inadequate estimates of divergence at low taxonomic levels, and limitations of the scope of the the biochemical method. Lorkovic, further limits the significance of enzyme electrophoresis to the study of populations and denies the possibility to delimit taxa with this method.

However, in his discussion Lorkovic does not analyse the real extent of the alleged discrepancies, the limitations and pitfalls of his method, or the problem of control data. There are also a number of misunderstandings of the electrophoretic approach and the interpretation of the biochemical data.

In this publication I analyze the Lorkovic paper and demonstrate the power of the biochemical-genetic approach.

Discrepancies between and results

Lorkovic (l.c.) compares the results of his crosses with the degree of enzyme dissimilarity (EDf) in his Table 1. (Note: The values given in Lorkovic's Table 1 are actually I-values, not EDf-values. A more appropriate statistic would be Nei's D (Nei, 1972) for the degree of genetic differentiation). We analyse here the statistical differences

between the results of the two approaches. For this investigation we use the correct value for the comparison between *Pontia daplidice* and *P. protodice* (I-value = .59, not .55; neither values have ever been published). We also disregard the fact, that Lorkovic (l.c.) has used his data of crosses between *Euchloe crameri* and the taxon *graeca* for the comparison of *crameri* and *simplonia* (electrophoretic data for *graeca* are not available, but there is unpublished evidence that *graeca* might be another species; this may be the reason for the observed differences between our results). Furthermore, *P. daplidice* in South Europe actually consists of two species (Geiger and Scholl, 1982a) and we use here the value for the comparison of species 2, the eastern european species, with *protodice* and *Pieris rapae* (these values were not available to Lorkovic, but the differences are small). If we calculate now the correlation coefficient for a linear regression between the two sets of data we find $r = .88$ (10dF) which corresponds to a $P < 1\%$. This is a very good fit and it seems unjustified to emphasize the differences. Of course this does not mean that there is absolute correlation for any individual comparison and the reasons for any observed deviations remain to be discussed. As Lorkovic (l.c.) already pointed out, such differences occur mainly at the lowest taxonomic ranks.

Advantages and disadvantages of enzyme electrophoretic methods

Enzyme electrophoresis is a method that allows one to compare populations and taxa using a set of genetic markers (loci). The zymograms obtained by this method make it possible to collect directly data on the genetic composition at individual loci. This means that different alleles at a locus can relatively easily be recognized. It is very important that the genetic interpretation of the zymograms is confirmed, if possible by analyzing the progeny of parents with various electrophoretic phenotypes, as with some enzymes additional bands may appear that have no direct genetic background (e.g. conformeric forms). For the Pieridae, an extensive analysis has been carried out on *Pieris brassicae* (Geiger, 1982). The pattern found corresponds perfectly with a simple Mendelian distribution.

If we are working with population samples of one or several taxa, we obtain two kinds of information: i) which alleles can be found at a locus in a population or in a taxon (qualitative information) and ii) in what frequencies (quantitative information).

The qualitative information can be used to investigate the distribution of alleles among populations. If we find e.g. a situation in which geographically separate populations of two taxa have different alleles at one or several loci, but share a common polymorphism at these loci in a zone of sympatry, it seems reasonable to conclude that the two taxa are in reproductive contact or have been so only a very short time ago. If we do not find such a common polymorphism in sympatry this is a strong

argument to assume interruption of gene-flow, and the existence of two species (e.g. Geiger and Scholl, 1982b; Geiger and Shapiro, 1986; Shapiro and Geiger, 1986).

As the genetic variants are easily distinguishable (they are, for all practical purposes, not detectably modified epistatically) the analytical power of such an investigation can hardly be reached with "classical" methods. The qualitative information obtained by means of enzyme electrophoresis also allows a cladistic approach (Ward, 1985). This has not yet been done for the Pieridae, but it is planned for the future.

Quantitative information: It is one of the advantages of enzyme electrophoretic methods that the degree of genetic correspondence between populations or taxa can be quantified. There are a number of different coefficients of genetic identity or distance that have been proposed during the last 20 years. In most modern investigations the statistic I for genetic identity or D for distance as developed by Nei (1972) and modified by Hillis (1984), are used. The D value $(D = -\ln I)$, used here, is an estimate of how many gene substitutions have been accumulated per locus since interruption of gene-flow between two populations or taxa. Of course, these values are strongly influenced by i) the choice of loci and ii) the number of loci investigated. Therefore, it is only possible to directly compare values of two different investigations in those rare cases in which an identical set of loci has been scored. The argument raised by Lorkovic (1.c.) that the fact that the values obtained in different systematic groups are different is a serious obstacle for the use of enzyme electrophoresis in taxonomy, is therefore only in part valid, as most investigators use different sets of loci. Thus, Lorkovic is perfectly correct when he states that the work of Racheli (1984) on *Parnassius apollo* cannot be directly compared with our analysis in the Pieridae, but this is only a problem if we want to relate the results of different studies. In all cases in which identical sets have been analyzed, as in our Pierid studies, the results are comparable

It has already been demonstrated (Geiger, 1981) that the levels of genetic identity found in different subfamilies of the Pieridae are in fact comparable. This is now confirmed by a much larger sample (over 100 taxa currently, all compared at the same 22 loci). However, how well do these levels correlate with the systematic rank of the taxa? Out of this large survey I have selected 42 taxa whose systematic rank is currently not seriously questioned and have related the D-values with the systematic rank. The result is summarized in Table 1. The outcome is an excellent agreement between the systematic rank generally used for the taxa and the D-value. Futhermore, most levels are nearly free of overlap; only between the levels of populations and subspecies as well as genera and subfamilies is this not true (see also Geiger and Scholl, 1984). Therefore, it seems justified to use quantified enzyme electro-phoretic data to discuss the systematic rank of taxa under review (Kitching, 1985)

This result found in the Pieridae is supported by similar investigations in other organisms (e.g. Avise, 1976). Once again, the important thing is not the absolute I- or D-value, but the correlation with the taxonomic rank.

I agree with Lorkovic (l.c.) that it is not possible to "prove" that a taxon is differentiated to the species level by using the I- or D-value alone. As I have already pointed out, a qualitative analysis of the genetic data may be conclusive in cases of sympatry. In allopatric taxa the degree of genetic differentiation may provide important arguments in the discussion of the systematic position of taxa with unclear rank. Again, the strongest clues in such situations may come from a qualitative analysis. There is little else one can do in such situations as the biological species concept can only be applied with some restrictions. This is exactly what we have always done when arguing at the species level. In most cases for which a substantial level of genetic differentiation has been found, this level is due to an unshared polymorphism or fixation of different alleles at one or more loci, rather then mere differences in allelic frequencies (Geiger, 1981; Geiger and Scholl, 1982 a and b; Geiger and Scholl, 1985; Geiger and Shapiro, 1986; Shapiro and Geiger, 1986). A similar analytical power could only be reached by a cladistic analysis of characters from "classical" or electrophoretic data. Such a cladistic analysis of classically used characters would also be the only real test for the genetic relationships evaluated by means of enzyme electrophoresis.

Another argument against the use of enzyme electrophoresis used by Lorkovic (l.c.) is that speciation probably does not take place due to changes at the loci covered by the electrophoretic approach. This is certainly true, but it should be clear now that we have good evidence that after the speciation event the taxa slowly accumulate changes at these loci. The argument is not the speciation occurs because of these alterations, but that due to the interruption of gene-flow after the speciation event we can very often find changes at the loci investigated. Therefore, it is also not important that not all the variation at the enzyme loci can be detected by routine investigations. Nevertheless, the amount of undetected variation mentioned by Lorkovic (l.c.) is only true for some extremely polymorphic loci not usually used in the Pieridae (Lewontin, 1986). For all other loci most of the variation is usually detectable.

A possible severe limitation for the electrophoretic approach may be that in rapidly evolving groups of taxa time was too short to result in distinct differences at loci covered with this method. It has to be expected that such cases will occur also in the Pieridae. However, it has to be pointed out again that there is no such case in the control data as yet. This is a clear sign that speciation events are generally reflected by accumulation of genetic differences at the set of loci used in the Pieridae.

The scepticism towards using these biochemical-genetic data to

evaluate systematics in the Pieridae also may have a historical reason. The first case in which I applied this approach in this family was the much debated European *Pieris napi*-group taxon *bryoniae*(Geiger, 1978). In this investigation it was not possible to detect any genetical differences between alpine *bryoniae* and lowland *napi*. This first analysis covered relatively few loci, but the results have since then been confirmed by a much greater number of loci (among them also the highly polymorphic esterases, Geiger, unpublished data), individuals, and taxa (Geiger, 1981; Geiger and Scholl, 1985). It is a remarkable result of this extensive work that genetic differences are very often greater among geographically close populations of *napi* as well as of *bryoniae* than between the two taxa. There was no other choice than to interpret these results as a support for those authors who argued for conspecifity of the two taxa. It lies in the nature of a disputed case that this conclusion was contradictory to the published opinions of others. But are the enzyme data really that much in opposition to the facts presented by such authors? To answer this question it is necessary to discuss the situation we encounter in the field and then the laboratory results. Eitschberger (1984), one of the most convinced proponents of the species rank for *bryoniae*, reports a significant number of hybrids found in the field. Similar observations have been made by others (e.g., Varga, 1967). This fact clearly demonstrates that gene-flow between *napi* and *bryoniae* is not interrupted under natural conditions even in Central Europe. Lorkovic (l.c.) points out that the two taxa show a reduced "hybrid fertility" in his laboratory crosses. This is certainly supported by data presented by Lorkovic (l.c.). However, his data also clearly show that there is some "hybrid fertility" even in the F2 crosses! The degree of this "hybrid fertility" is remarkably high, especially in the black-crosses (R1, see Table 2, Lorkovic, l.c.) which clearly means that the laboratory results confirm the observation of gene-flow in nature (morphologically intermediate individuals). The enzyme data strongly support this view indicating that there is no sign of an interrupted reproductive contact. Clearly, a certain degree of reduced fertility can be observed, but it seems safe to state that the data from different approaches are not as contradictory as they have been presented; the opposite is true. To solve the nomenclatural problem I propose to take advantage of the rules in the new edition of the "International Code of Zoological Nomenclature" (1985). We now have the possibility to take into consideration a somewhat reduced degree of fertility, and rank such a taxon as a semispecies. This is also exactly what Lorkovic (1962) has done in earlier papers.

Interspecific hybridization and phylogenetic relationships

In his publication Lorkovic (l.c.) uses his data from laboratory interspecific hybrid crosses to test the enzyme electrophoretic data. The basic philosophy behind the use of these hybridization results to evaluate

phylogenetic relationships is the speculation that after interruption of gene-flow the taxa gradually accumulate characters that directly affect the degree of genetic incompatibility. However, to use his method as a test for the enzyme electrophoretic data Lorkovic should first demonstrate that the results from the interspecific crosses in the Pieridae are in fact strongly correlated with the phylogenetic relationships. This has not been done and is no easy task, the reason of course being that we are dealing with a historical process and there is no method available to reveal unequivocally the real course of evolution. There are some methods (like cladistic analysis) that have a high potential to do so, but all methods have their pitfalls. All we can do is to try to apply as many methods as possible and find the most parsimonious family tree. Again, it has to be pointed out that the high correlation between Lorkovic's data and the enzyme electrophoretic analysis is highly encouraging and should be the basis for future investigations. A third approach with a potentially high power of resolution would be a cladistic analysis, but such an analysis is not available for the Pieridae.

One case for which our approaches give different values of evolutionary distance has already been discussed (*Pieris napi/bryoniae*). There are two more such cases: *Euchloe crameri/simplonia*, and *Pieris rapae/mannii*. To discuss these we first have to analyse possible problems and limitations of the interspecific hybridization approach.

I) The interspecific hybridization approach as presented by Lorkovic (l.c.) works uniquely with postcopulative isolating mechanisms. All precopulative factors that prevent gene-flow between taxa such as olfactory, behavioral, ecological, and partly morphological incompatibilities are excluded by this approach since the usual method of mating is hand-pairing. The importance of such factors should not be underestimated. Strictly speaking, by this method, it is only possible to compare taxa that have only developed postmating isolating mechanisms, yet much effort should be devoted to evaluating both pre- and postmating barriers. Such premating isolating factors seem to be the reason for the discrepancies in at least one of the above mentioned cases: *Euchloe crameri* and *simplonia* (again, Lorkovic used *graeca* instead of *simplonia*, a fact that itself may account for the differences). Lorkovic (l.c., p.345) himself mentions that there is a well-expressed premating barrier between these two taxa. Taxa that are separated by such mechanisms do not need to develop additional strong postcopulative mechanisms (Mayr, 1963). The approach used by Lorkovic (l.c.) will in such cases underestimate the degree of genetic differentiation. On the other hand enzyme electrophoresis measures the accumulated differences since interruption of gene-flow regardless of the true nature of isolating mechanisms. Therefore, it seems unjustified to solely blame enzyme electrophoresis for the observed differences in the results of the two approaches in the sense of not revealing the true degree of genealogical relationships. Moreover, as most of the populations of the

two taxa are allopatric, relatively weak isolating mechanisms seem to be sufficient to maintain genetic identity (this is also an important problem for the hybridization approach in clear-cut allopatric taxa, especially in taxa from different continents, islands, or mountain ranges. In such situations theoretical problems in applying the biological species concept also arise).

A similar problem may be the basis for the differences in the results of the comparison of *Pieris rapae/mannii*. These two taxa are sympatric in large parts of their recent distribution area. To avoid gene-flow and maintain identity as distinct species the two taxa have obviously developed strong postmating isolating factors. This does not mean that speciation occured because of the same factors. The degree of hybrid sterility will in such situations tend to overestimate the phylogenetic distance. Furthermore, it should be noted that strong hybrid sterility may be caused by mutations at one or a few loci and need not reflect profound genomic differences. Complete sterility among strains within a species may also occur due to transposable elements (hybrid dysgenesis in *Drosophila*, Kidwell et al., 1977; Engels, 1983) or as a consequence of an infection by a microorganism (*Tribolium*, Wade and Stevens, 1985).

II) I have already mentioned several times the fact that enzyme electrophoresis is primarily a method to estimate the time passed since interruption of gene-flow (Berlocher, 1984; O'Brien et al., 1985). There is good evidence that this is also true for the Pieridae, one indication being the non-overlap of the levels of genetic differentiation (Fig. 1). To make the hybridization data comparable one would have to demonstrate that the factors used by Lorkovic (l.c.) such as "size", "number of offspring", "development" and "inviability" are also correlated with the phylogenetic age of the taxa. Furthermore, the proposed quantification of these factors needs also to be tested for this correlation.

III) The interspecific hybridization approach as used by Lorkovic (l.c.) works with individual, essentially randomly-selected animals, not populations. The numbers of comparions are in many cases very low. Therefore, it would be highly important to know more about the reproductive success of randomly chosen individual butterflies. Our own observations among European and North-American taxa show that the degree of fertility, even among individuals of one population, may vary enormously and may be different among taxa. In other words, we first have to know more about the variance of fertility among individuals of local populations before we can quantify such rates among taxa. In some critical cases there should even be a detailed analysis comparing the fertility among individuals of geographically distant and close populations and especially within a zone of contact. Unfortunately, the amount of labor required to do such an analysis may often be prohibitively great. Nevertheless, there are investigations that use this approach (e.g., Oliver, 1978).
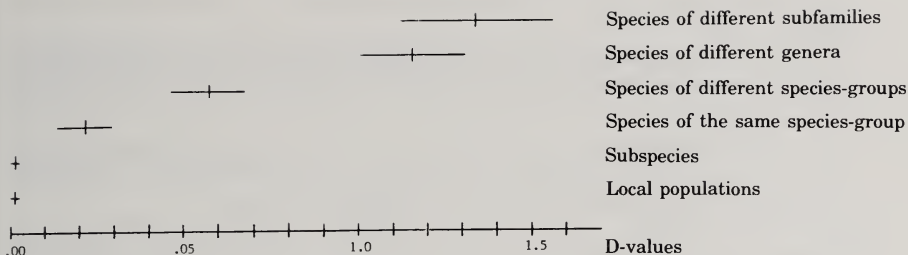
Fig. 1. Levels of genetic differences among 42 taxa whose systematic rank is currently not debated (22 loci)

Conclusions

It was the purpose of this publication to continue the discussion on how best to estimate the degree of the phylogenetic distance between taxa. It has been concluded that it can not be inferred from the observed differences between the results of the interspecific hybridization and enzyme electrophoretic approaches that the latter method gives inadequate estimates. In fact such differences only occur in some much-debated cases for which there are good reasons to assume that the first method may over- or underestimate the phylogenetic age of the taxa discussed. It has been demonstrated in a set of Pierid taxa whose systematic rank is generally not questioned that enzyme electrophoretic data are highly correlated with the systematic rank of the taxa. The generally good agreement between the results of the two approaches is regarded as highly encouraging for future analysis.

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Systematics of *Ascia* (*Ganyra*) (Pieridae) Populations in the Sonoran Desert

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Abstract. A breeding population of *Ascia* (*Ganyra*) (Lepidoptera: Pieridae) in the *josephina* complex is confirmed for Arizona. The larval hostplant is found to be *Atamisquea emarginata* Miers., a plant confined to the Sonoran Desert.

This population, while closely related to *Ascia josephina josepha*, is distinct in maculation, androconial pattern, genitalia, and larval host. Its taxonomic status is discussed. Full species status is given to the insect as *Ascia howarthi* (Dixey).

Introduction

During the course of a study for the National Park Service on arthropods of the Quitobaquito Management Area in Organ Pipe Cactus National Monument (OPCNM), Pima County, Arizona, the author discovered an apparent population of a pierid butterfly in the *Asia josephina* (Godart) complex. The discovery is noteworthy in that records of this species complex are scarce in Arizona, in that the insect appears to be breeding in the area, and in the distinct phenotypes of the population.

The genus *Ascia* is divided into two subgenera, each represented by a single Nearctic species or species complex (Howe, 1975). An additional taxon, *A. sevata* (C. & R. Felder), is recorded in Mexico. The subgenus *Ascia* includes the species *monuste* (Linnaeus) and its subspecies. The subgenus *Ganyra* Billberg includes the species (or species complex) *josephina* (Godart) with its Central and North American subspecies *josepha* (Salvin & Godman), *howarthi* (Dixey), and *kuschei* (Schaus) and it also includes the species *sevata*.

Only *josephina josepha* from *Ganyra* has been cited within the United States (Pyle, 1981, et al.). However, the recent studies at Quitobaquito, OPCNM confirm the presence of an Arizona population of the *josephina* complex and suggest assignment outside the subspecies *josepha*.

This paper examines the dimensions of the Arizona *Ganyra* population and its relationships with other populations in the *josephina* complex. It links the Sonoran Desert *Ganyra* population to a specific larval foodplant and alters the taxonomy of the species complex.

A series of both sexes of adults of Sonoran Desert *Ganyra* was collected from several wild populations. Those were further augmented by specimens from the San Diego Natural History Museum, the California Insect Survey collection, and the private collection of Kilian Roever. A

small series of *A. josephina* from southern, eastern, and western Mexico, as well as Texas, was also obtained. The Texas A & I collection and the private collections of J. Brock, D. Mullins, and P. Hubbell were also used. Steve Prchal of the Arizona-Sonora Desert Museum photographed all stages of the life history. Measurements were done using a Lassico Ocular Filar. An ISI-DS-130 scanning electron microscope at the University of Arizona campus was used for the micrographs.

Taxonomy

Most of the taxa in the *A. josephina* complex were originally described in the genus *Pieris* Schrank. They were later placed in the genus *Ascia* Scopoli and still later in either the genus or subgenus *Ganyra*, depending on the author. Godart described nominate *josephina* in 1819 from the Antilles, probably Haiti and Cuba (Salvin & Godman, 1868). It is characterized by the large size, falcate forewing, and a large black forewing discal cell-spot. Two other closely related Antillean subspecies have been described: *paramaryllis* Comstock from Jamaica, and *krugii* (Dewitz) from Puerto Rico. Both of these are somewhat smaller, with the characteristic black forewing cell-spot narrow (Comstock, 1943).

The subspecies *josepha* (Salvin & Godman) is the widespread Mexican and Central American form. It differs from nominate *josephina* primarily in the shape of the wings. The forewings are not as falcate as those of *josephina* and the hindwings are more squared and less produced at the anal angle. It occurs from southern Texas (straying northward to Kansas) through eastern Mexico into Central America and north along the west coast of Mexico into Sinaloa.

Dixey (1915) described subspecies *howarthi* from Baja California Sur, Mexico. He described it as having more noticeable marginal spotting on the forewing and more pronounced reticulations on the ventral hindwing than typical *josephina*, as well as being comparatively small (males 58 mm wingspread, females 52−54 mm).

Schaus (1920) described *kuschei* from Mazatlan, Sinaloa, Mexico. It is characterized by a greater extent of the submarginal maculation on the forewings in both males and females. He cited both sexes as having wingspreads of 56 mm which is considerably smaller than typical *josephina*.

Felder & Felder (1861) described the taxon *sevata* from Venezuela. Rindge (1948) cited the Baja California population of *Ganyra* as *A. sevata kuschei*, a new combination at that time. The original description of *sevata* mentioned a solid white dorsal surface except for the apical marginal border, wider in females than in males. Fruhstorfer (1908) subsequently named a more northerly subspecies, *A. sevata tiburtia*, from Guatemala. It differs from true *sevata* in the narrowing or absence of *A. sevata*'s 5 mm forewing border. The ventral hindwings of *A. sevata* and *A. tiburtia* are also suffused with shades of violet and pink respectively. No mention of forewing cell-spots is made for either taxon.

There are obvious close superficial relationships among the various members of the subgenus *Ganyra*. A closer look will now be given to the exact relationships between those taxa (north of Guatemala) and where the OPCNM population lies in reference to them.

Several key points suggest that *A. sevata sevata* and *A. s. tiburtia* are more distantly related to the *josephina* complex. The lack of the black forewing cell-spot does not in itself suggest removal from the group since Cuban, Jamaican, and Puerto Rican populations of *josephina* also have this spotting weak to non-existent (Comstock, 1943). However, the presence of a narrow to wide continuous forewing border and pink to purple ventral hindwing coloration do set these taxa apart. More importantly, there are significant differences in the form of the male androconia. These average only 0.24 mm in length in *sevata*, approximately half that of the *josephina* complex members (Dixey, 1915). Hoffman (1976) cited *tiburtia* from southern Mexico, a range overlapping that of *josepha*. This sympatry suggests distinction at the specific level. *Sevata* is here considered outside the *josephina* complex.

The relationship between *A. howarthi* and *A. kuschei* needs clarification. Although *kuschei* was described from Mazatlán, it appears to have been collected far north of there. There are many recent records of a *Ganyra* from the Mazatlán area, all of which represent *josepha*, not *kuschei*. The maculation, androconia, and size are all consistent with *josepha*. The location "Mazatlán" was probably used in a broad sense by Kusche. Phenotypes matching the *kuschei* description occur from extreme northern Sinaloa northward, where he easily may have collected. Many specimens from Sonora and Arizona, and a few from Baja California closely match the *kuschei* description, especially for broods during the summer rains. The type locality for *kuschei* should probably be amended to San Miguel, near Los Mochis, Sinaloa, Mexico, the southernmost locality for which that taxon is known. The *howarthi* phenotype, at least ventrally, is restricted to Baja California. But other phenotypes with unmarked ventral hindwings also occur there. These unmarked phenotypes are also widespread in central and northern Sonora and represent the majority of the specimens taken at OPCNM. The three phenotypes — heavily marked *kuschei*, ventrally marked *howarthi*, and the unmarked population — all blend with each other. Also, the OPCNM population was reared on a Sonoran Desert shrub, *Atamisquea emarginata* Miers., in the family Capparidaceae. When mapped together, the distribution of the three phenotypes duplicates that of the probable hostplant, *A. emarginata* (Fig. 1). *Kuschei* and *howarthi*, plus the unmarked phenotype are therefore considered synonymous. Similarities in size, androconial pattern, and the distribution of the larval foodplant all suggest this. Since *howarthi* has priority, the name *kuschei* is suppressed as a junior synonym.

The third clarification necessary is the relationship between *josepha* and *howarthi*. On the basis of size, *howarthi* and *josepha* represent two
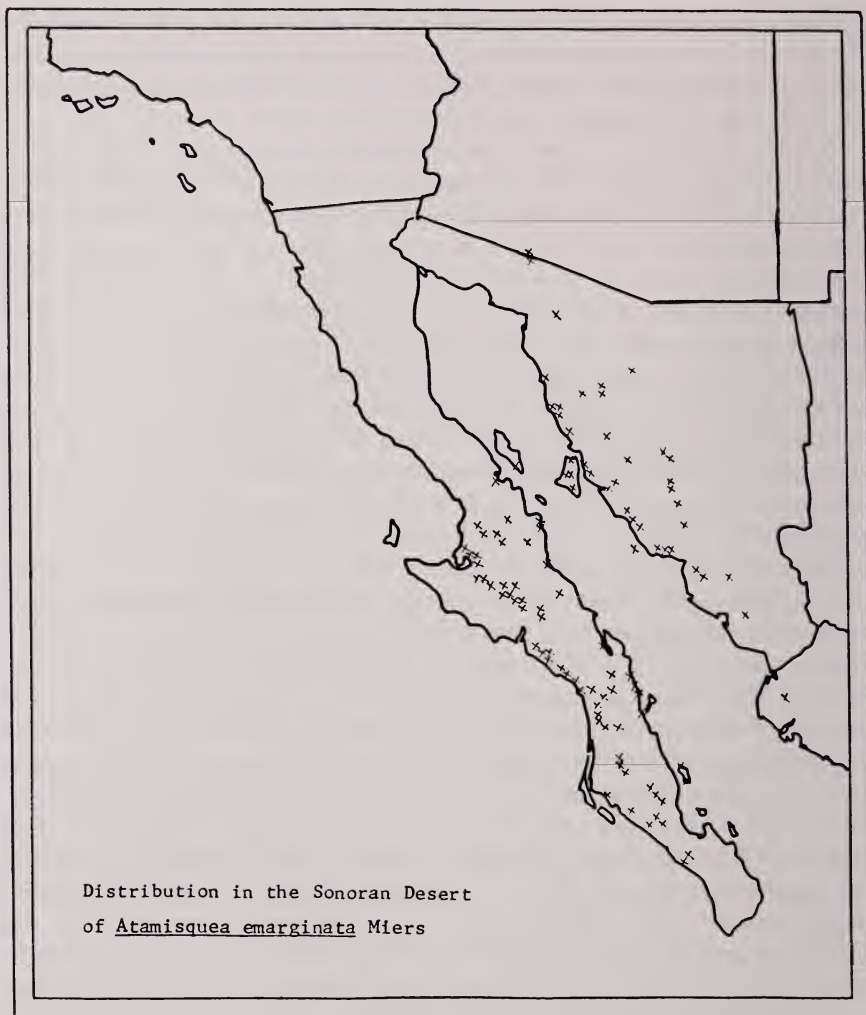
Fig. 1.   Distribution of *Atamisquea emarginata*, probable larval host of *Ascia howarthi*.

very different populations. Both sexes of *howarthi* average in excess of 10 mm smaller in forewing length than those of *josepha*. There is no size overlap in the males and only a single small female *josepha* overlaps the size range of female *howarthi*. The size mentioned for *howarthi* by Dixey (1915) seems inflated. He cited the male wingspread as 58 mm but the male figured is only partially spread. His figure has a 55 mm wingspread with a 26 mm forewing length. In contrast, a well-spread specimen with a 26 mm forewing length has only a 45 mm spread.

   The wing shape is also different in the two taxa. In *howarthi*, the forewings are somewhat shortened and the hindwings are very rounded. In *josepha*, and apparently even more so in nominate *josephina*, the

forewings are produced or even falcate while the hindwings have the anal angles extended (Figs. 2–5).

In their maculation, the males of *howarthi* are generally more heavily patterned than those of *josepha*, especially with forewing marginal and submarginal spotting. Females are very similar in the two taxa, but in *josepha* dark morphs are often produced where the ground color is heavily overlaid with cinnamon brown. All specimens of this morph seen were mid-summer captures and probably parallel the long-day form of *Ascia monuste* (Pease, 1962). The absence of dark morphs in *howarthi* is interesting in light of the paucity of records away from breeding colonies (Fig. 6). Both sexes of *howarthi* have an additional diagnostic mark on the ventral hindwing. Aside from the dark scaling distal to the cross-vains at the base of cells M3 and Cul, there is a darker spot on and around the cross-vein at the base of cell M2. While males of *josepha* will rarely have that cross-vein darkened (even dorsally) it is not scaled away from the vein as in *howarthi*.

While the androconial scales of *howarthi* and *josepha* are similar in size and configuration (Dixey, 1915), their placement on the wings is vastly different. All androconia of *howarthi* are confined to forewing cells M3, Cul, Cu2, and 2A (Fig. 4). On *josepha*, the androconia in these cells are far more extensive. In addition, scent scales are present in cells M2, M1, and the discal cell. Furthermore, *josepha* invariably has androconia on the hindwing as well, in cells RS, M2, M3, the discal cell, and occasionally in Cul.

The general configurations of the male genitalia of both taxa are similar. Due to the larger size of *josepha*, the entire genital capsule is larger in that taxon than in *howarthi*. However, the length of the saccus

Ascia howarthi   *Ascia howarthi*   *Ascia howarthi*

Ascia josepha.   *Ascia josepha.*   *Ascia josepha.*
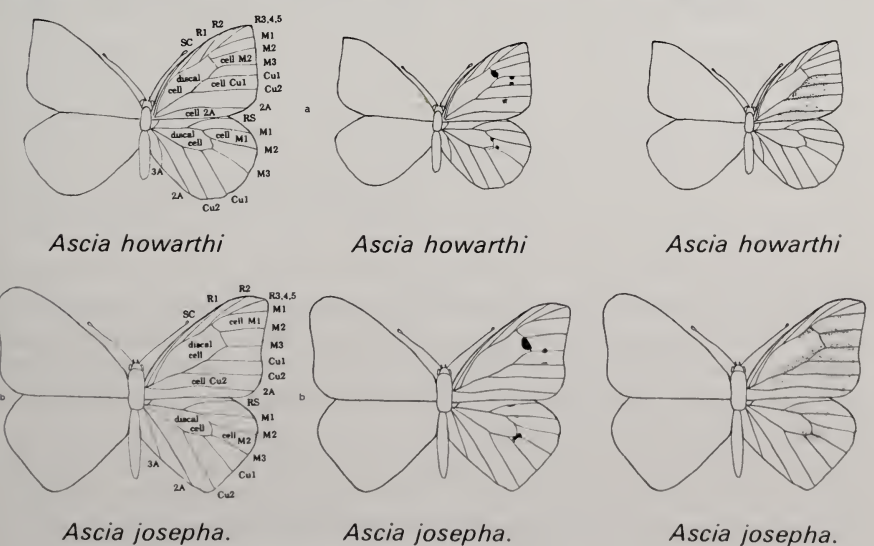
Fig. 2.   Venation   Fig. 3.   Ventral maculation Fig. 4.   Androconia pattern
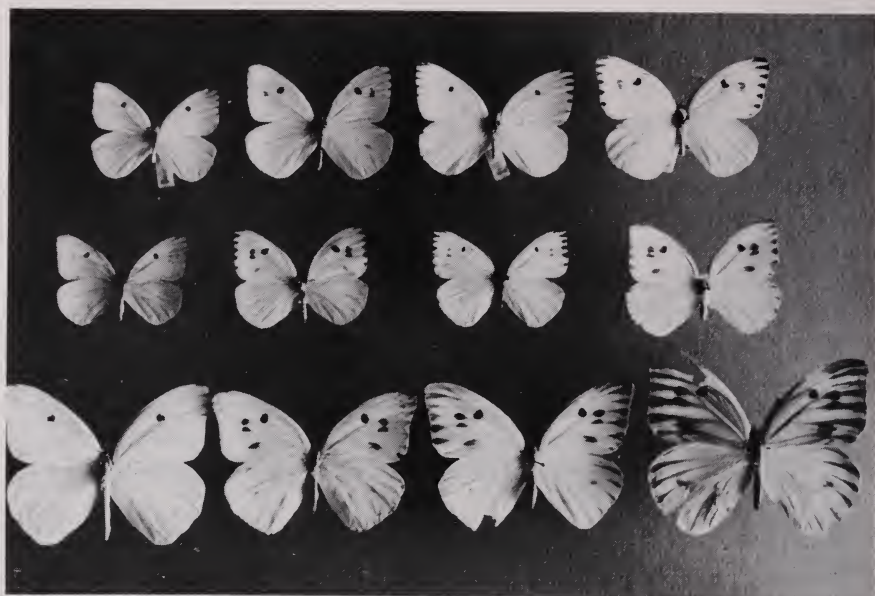
Fig. 5.   Phenotypic range of *Ascia howarthi* (top two rows, males above, females below) and *Ascia josephina josepha* (bottom row).

is proportionately greater in *howarthi* than in *josepha*. Likewise, the aedeagal elbow (Fig. 7) of *josepha* is proportionately larger than that of *howarthi*. These genitalic differences are present but best used cautiously.

For the genus *Ascia*, members of the families Cruciferae, Capparidaceae, and Batidaceae have been reported as hostplants (Howe, 1975). More specifically, *Capparis frondosa* Jacq. was cited as a hostplant for *A. josephina josepha* (Jordan, 1981). Although this caper is confined to the eastern slope of Mexico, mostly Tamaulipas and Veracruz (Standley, 1961), other members of the genus have wider distributions in Mexico and probably serve as foodplants in other parts of the range of *josepha*. Members of the genus *Capparis*, whose distributions include Sinaloa, are *C. flexuosa* L., *C. verrucosa* Jacq., and *C. indica* (L.) (Standley, 1961). Any of these might serve as larval hosts for *josepha* since the northern distributional limits of the plant and insect appear to match one another. None of the members of the genus *Capparis* has been reported as far north as Sonora. Records for *josepha* extend north to Mazatlán, Elota, and Guamuchil, approximately 100 km southeast of Los Mochis in northern Sinaloa.

Records of *howarthi* extend south into northern Sinaloa, near Los Mochis. This brings the two taxa within 100 km of each other. In fact, a somewhat questionable record of a dark morph female *josepha* taken near Alamos, Sonora would bring the two populations into overlap. The lack of an apparent cline or anything resembling intergrades suggests a high integrity and differentiation between the two populations.
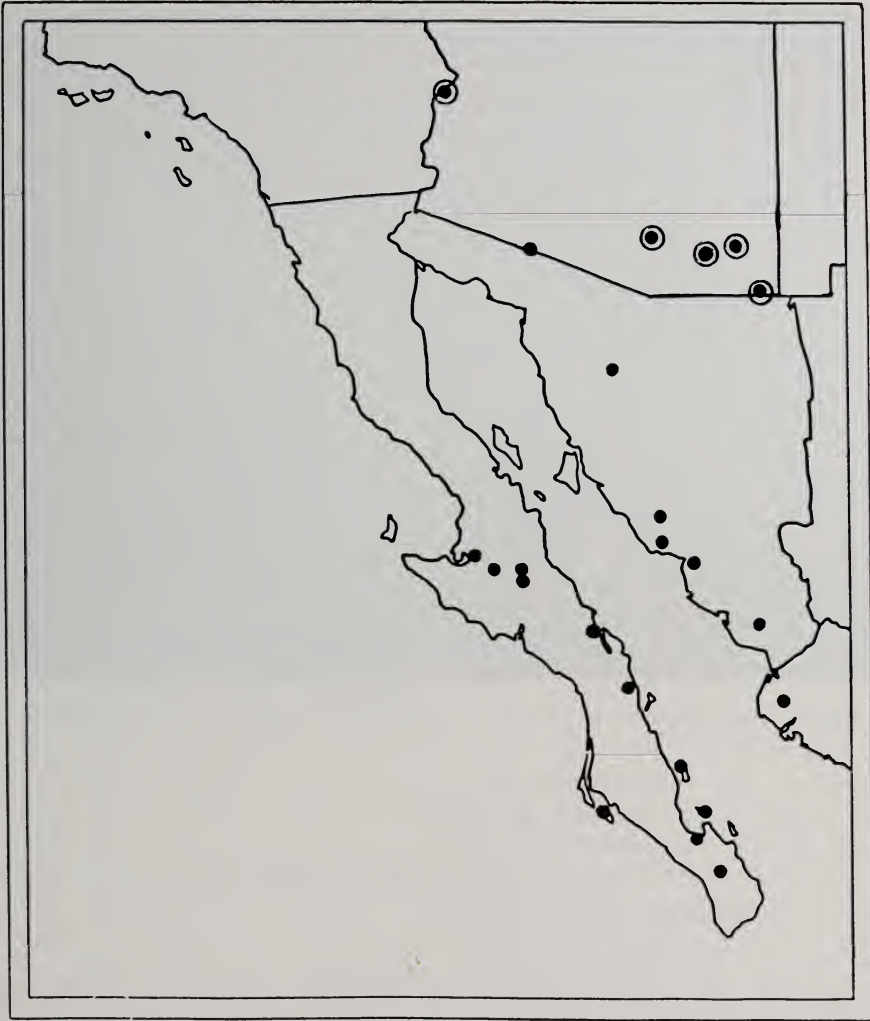
Fig. 6.   Distribution of *Ascia howarthi*.

This differentiation between the Sonoran Desert *Atamisquea*-feeding *howarthi* and the *Capparis*-feeding *josepha* of the remainder of Mexico persists even when *howarthi is compared to josephina* as a whole. It therefore appears that the differences are at the species level, not at the subspecies level. Therefore, I propose to elevate the taxon *howarthi* to species status. It is most closely related to *A. josephina*, less so to *A. sevata*.

The genus north of Guatemala and exclusive of the Antilles would be composed of four species as follows:

Genus: Ascia Scopoli

        Subgenus *Ascia* Scopoli

Fig. 7.   Aedeagus of *Ascia howarthi* showing "elbow" to left of center.

1. *monuste* (Linnaeus)
   a) *monuste* (Linnaeus)
   b) *phileta* (Fabricius)
   c) *cleomes* (Boisduval & Le Conte)
Subgenus *Ganyra* Billberg
2. *josephina* (Godart)
   a) *josepha* (Salvin & Godman)
3. *howarthi* (Dixey)
4. *sevata* (C. & R. Felder)
   a) *tiburtia* (Fruhstorfer)

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On *Pieris (Artogeia) marginalis macdunnoughii* Remington (Pieridae)

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Abstract. Some previous work on *Pieris (Artogeia)* ssp.*macdunnoughii* and ssp. *marginalis* is summarised. Experiments in which Colorado *macdunnoughii* were hybridized with European P. *napi* L. are reported, with particular attention to inheritance of yellow pigmentation and viability of F_1 hybrids: no females are obtained from *napi* ♀ × *macdunnoughii* ♂. *Macdunnoughii* carries two distinct systems of yellow coloration, both the bisexual recessive sulphurea and the female-limited dominant flava. Whether this unusual condition has any ecological or evolutionary significance is uncertain. It is concluded that neither subspecies *marginalis* nor *macdunnoughii* is conspecific with the typical *napi* of Europe, but Eitschberger's opinion that *macdunnoughii* is a subspecies of a species *marginalis* Scudder may well be correct. However, the relative position of the subspecific taxa *venosa* Scudder, *microstriata* Comstock and *mogollon* Burdick requires experimental investigation.

Introduction

This Colorado subspecies was described as of *Pieris napi* L. by Barnes & McDunnough in 1916 under the name *pseudonapi*. The type-locality was "Silverton, 10,000 ft., where it is single-brooded". The description as very close to European *napi* "although in the females the black dots of the primaries are practically obsolete" is very meagre for a subspecies; the females varied in the amount of black markings. The completeness of the picture is improved if we can add the authors' description of *pallidissima*, the second generation at Provo, Utah, which they seem to have regarded as consubspecific with *pseudonapi*.

Remington (1954) pointed out that the name *pseudonapi* had been used by Verity (1911) for a race of *Pieris melete* Ménétriès, and re-named the Colorado insect *P. napi macdunnoughii*. He added that the series of *Pieris napi* at Yale University from Colorado, Utah, Nevada and Wyoming [i.e. the populations considered as subspecies *macdunnoughii* and ssp. *pallidissima* by Eitschberger 1983] indicate that all represent a single race. He says, "My series from the Teton Mountains of Wyoming shows very dark and very pale individuals taken flying together" — one supposes that the reference is to melanic markings, not to any yellow pigmentation. I conclude that Remington, like Barnes & McDunnough before him, regards *macdunnoughii* and *pallidissima* as showing no differentiation worthy of separate subspecific naming.

Eitschberger (1983) treats these populations as separate subspecies of a species *Pieris marginalis* Scudder, which is said to include also *mogollon* Burdick (New Mexico) and six newly named subspecies as well as ssp. *marginalis* (Washington Terr.) and perhaps *hulda* Edwards (Alaska).

Warren (1963), working from androconial scales, had attributed ssp. *marginalis* to *napi* and ssp. *macdunnoughii* to a species *oleracea* Harris, but the present writer is inclined to follow Eitschberger in respect of these two subspecies, if only on account of their special pigmentation.

The Ssp. *marginalis*

In 1970 I reported experiments in which a N. W. Oregon (Saddle Mt. State Park) stock of *"Pieris napi marginalis"* was crossed with the bright yellow British *napi* form sulphurea Schöyen (Head's "citronea") and with certain other European forms. The Oregon insects were yellow in ground-color: very faintly citron-shaded in the males but deeper in the females. The markings of the latter sex differed from those of *napi* by the often unequal development of the melanic markings: though the fore-wing hind-marginal streak was generally present, the second and even more the first discal spots were much reduced and often absent.

The breeding results seemed to indicate that the population was homozygous for an intermediately recessive gene of the subtalba-sulphurea series (Bowden 1963), indistinguishable from that producing "Thompson's pale yellow" rarely in the British Isles. The conclusion then was that "pale yellow" heterozygotes should be sought in other American subspecies of the napi *group*: it was hardly expected that other homozygous populations would be found, but *macdunnoughii* might perhaps be polymorphic in respect of sulphurea?

However, the flava (ochreous) color whch was found in the F_1 *napi*-hybrid females was then attributed to the European parents and it was not realized that the *marginalis* stock might also carry some flava. But Shapiro (1985, *in litt.*) had noticed that some *marginalis* populations had high frequencies of a buff female. Looking at the 1970 *marginalis* specimens now, it seems beyond dispute that the females possess an ochreous tinge as well as the lemon, and that the F_1 hybrid females' color is unlikely to have come entirely from the European side.

The Ssp. *macdunnoughii*

In 1971 I reared only two females of this subspecies from Gunnison Co., Colorado (W.B. Watt). They were caged with two (later four) English (Herts.) males, but these paid no attention, though brothers were pairing with other butterflies in nearby cages. After two days three (later five) Scottish males were supplied, but again showed no concern. A male from French Pyrenees showed minimum interest. It appeared that at least these two individual females had no pheromone attraction for European males.

Not until 1985 were we able to raise *macdunnoughii* in adequate numbers (brood 1985-*r*), by pairing offspring of females taken in Grand Co., Colorado, in 1984 (Shapiro). We found that the fresh females were definitely a greenish yellow (very near the color of the forewings of *Gonepteryx rhamni* L. ♀), the males very palely yellow, but quite distinct from the white of *napi*. Apart from slight forewing apical blackening, our males were typically without marking, and the females carried only the forewing discal spot that normally marks *napi* males; even this was sometimes absent and the hind-marginal female streak hardly ever showed at all.

Thus comparing the markings of these two subspecies with those of typical *napi*, the females departed from type in opposite directions: the expression of *marginalis* forewing markings was biassed posteriorly, those of *macdunnoughii* even diminished in that direction.

Experimental

Macdunnoughii males of brood 1985-*r* paired in August 1985 with British *napi* f. sulphurea females, but the mere 15 eggs produced only nine pupae, of which six (presumably female) proved unable to develop. One male hybrid emerged normally in September, a very pale lemon yellow, with faint black forewing apices and spots, and very slight veining below. Two more pupae colored as males and split their thoraces but failed to eclose: these were dissected out and appeared similar to the first male. This rather disappointing result, as far as it goes, does indicate that the *macdunnoughii* lemon tint, like that of *marginalis*, belongs to the sulphurea series of alleles.

Three other pairings of *macdunnoughii* males (one from 1985-*r*, two from the subsequent inbred 1985-*q*) were made with single *napi* females of mainly European stock (which however carried some genes derived from ssp. *oleracea* and were of funebris form — see Lorković 1971, Bowden 1983). The resulting broods (1985-*k*, 1986-*g*^{i}, *g*^{ii}) were large, but nevertheless only male hybrids emerged, even after diapause; their upperside ground-color was uniformly pure white, without yellow toning, as expected from heterozygous sulphurea. There was indeed one female in *g*^{ii}, but this was rejected. (*Marginalis* and *macdunnoughii* hybrids with *napi* usually carry radiating black markings on the distal ends of the veins. Such are uncommon on pure ssp. *napi*, and *napi* waifs can thus be recognised, though without certainty.) The melanic pigmentation of the hybrids may be described and discussed later.

The apparently more difficult reciprocal hybridization was obtained in August 1986, using a funebris heterozygote male of 1985-*h*. The *macdunnoughii* female came from brood 1985-*q*. It was expected that in this case female hybrids would precede the males, if the apparent sexual imbalance in the earlier hybrids was due to a disturbance of diapause control. In this brood, 1986-*n*, losses of larvae in early stages were appreciable, probably 15-20%. Twenty males emerged 14-21.ix.86,

followed by a mixture of 19 ♂ + 25 ♀ by 23.x.86, giving a final ratio of 8 ♂ : 5 ♀. A few other pupae died.

Surprisingly, all the F_1 hybrid females were of a light yellow color, rather with a flava tinge, and none were very near white. Thus this color was inherited from the *macdunnoughii* mother in the dominant mode, and was expressed only in the females.

It was thought unlikely that a straight F_2 hybrid brood would be productive. Males of the first F_1, 1985-*k*, were back-crossed in each direction:

♀♀funebris hz., 1985-*h* × ♂♂ 1985-*k* → 1986-*c*, 33 ♂ + 24 ♀,
♀ *macdunnoughii*, 1985-*r* × ♂ 1985-*k* → 1986-*j*, 5 ♂ + 3 ♀,

the sexes here being not significantly far from equality ($\chi^2 = 1.4$, p = 0.23 and $\chi^2 = 0.5$, p = .90 respectively). Brood 1986-*c* gave 57 adults the same year. All the males were white, as were some of the females, others varying from slightly tinted up to near a full flava color in two cases. The pigmentation here was definitely not of the sulphurea series, and as the brood had two mothers, a ratio 2 flava: 22 no-flava would be meaningless. Fifteen individuals of 1986-*c* were funebris (though of varying expression), almost exactly the anticipated number.

The other back-cross 1986-*j* resembled pure *macdunnoughii* in respect of wing ground-color: tinted citron even in the males, very definitely so in two of them. The one white male was small (2×19 mm), but the other seven insects were large. The striking markings of several females, possibly influenced by the funebris gene, may be discussed in a later paper.

Pigmentation Systems

More than thirty years ago (1954) I was able to write of general agreement that there were at least two distinct forms of *napi* with extra yellow on the wings: ochreous flava Kane confined to the female and with the color *not* extending to the forewing disc underside, and the primrose sulphurea Schöyen with the more extensive bisexual coloration. Thus all the *Pieris* butterflies with yellow wing-uppersides have since been interpreted in terms of these two modes:

female only — brownish — dominant or semi-dominant genetically
bisexual — citron yellow — recessive genetically.

So the tests are:

if a problem male (white or yellow) crossed with a sulphurea female *napi* produces any yellow sons, it carries sulphurea;

if a problem female (yellow or ochreous) crossed with a sulphurea male *napi* produces any yellow sons, it carries sulphurea; if only white sons, it carries flava;

if a problem female crossed with wild-type *napi* produces any yellow daughters, it carries flava,

provided that numbers are adequate.

In both flava and sulphurea the saturation of the color can vary from very faint to intense, sometimes by the action of different alleles (cf. Bowden 1961) and sometimes environmentally. Some sulphurea alleles give only a *very* faint coloration to male butterflies: in all doubtful cases the forewing underside disc should be examined (Bowden 1961). Also, the sulphurea color is particularly liable to fade, especially in sunlight. At paler levels visual discrimination between flava and sulphurea becomes more uncertain.

It was known that both kinds of color could occur together in the same individual — Bowden (1962) described the transference of sulphurea genes to *P. (napi) bryoniae* Ochsenheimer. Unfortunately I never considered that any natural population might constantly use a combination of the two systems of pigmentation. It was thus that I came partly to misinterpret the Oregon *marginalis* coloration.

When the pigments do co-exist in uncertain proportions in the females of a species they are difficult to distinguish visually, even in a fresh specimen. Photographic rendering a usually imperfect. If the flava and sulphurea systems are acting together in a population with yellow males, it is possible to identify them by hybridizing with *napi* carrying neither flava nor sulphurea. The result in the F_1 should be white males plus ochre-tinted females. This is the result obtained with both *marginalis* and *macdunnoughii*, which therefore carry flava as well as sulphurea.

Is the matter therefore to be considered closed? Perhaps not quite. Though sulphurea and flava pigments are generally separable by eye, chemical composition within each class may not be constant, and genetic controls in these Pierids may involve more than two loci.

Moreover, some biological aspects of the situation remain puzzling. Have these fainter colors *any* ecological effect? Do they offer clues to the phylogeny of taxa carrying them? Bowden (1977) figured a female *macdunnoughii* extremely reflective of U.V. light, indeed much more so than *marginalis*, but this phenomenon needs wider investigation in N.W. American *Artogeia*.

Specific Status

How distinct from *Pieris napi* L. is ssp. *macdunnoughii*? And how close to ssp. *marginalis*? The pterin pigmentation systems of these two subspecies are so similar as to suggest a close relationship. How do they react to hybridization with the European species?

Male *napi* have seemed rather unwilling to pair with *macdunnoughii* females, but one cage pairing occurred within a quarter of an hour. The reciprocal pairing is easy. In either case fertility is very good.

But the three large broods ♀ *napi* × ♂ *macdunnoughii* produced no F_1 daughters (the one female obtained showed no characters negating a pure *napi* origin and was probably a waif). The one brood 1986-*n* from

♀ *macdunnoughii* × ♂ *napi* yielded both sexes, but females were the less numerous (40%) and generally appreciably smaller; their fertility was not tested.

It is appropriate to compare the results for the *marginalis* × European hybrids reported in 1970:

napi ♀ × *marginalis* ♂ → 1968-*b*, 7 ♂ + 1 ♀ + 15 undeveloped pupae,
marginalis ♀ × *napi* ♂ → 1968-*a*, 9 ♂ + 8 ♀ (incl. 1 ♂ after diapause),
Irish *napi* ♀ × *marg.* ♂ → 1966-*i*, 38 ♂ + 1 ♀ + 15 undeveloped pupae,
marginalis ♀ × Irish ♂ → 1968-*j*, 32 ♂ + 39 ♀.

They agree very well with those quoted above for *macdunnoughii*: on the whole it can be said for both ssp. *marginalis* and ssp. *macdunnoughii*, the cross ♀ *napi* × ♂ *m.* produces no viable female offspring — it is only too likely that the single females in 1968-*b* and 1966-*i* were waifs.

Such a sexual disturbance is more serious than a diapause disorganization, and is normally sufficient ground for a specific separation (cf. Lorković 1978). One could, however, expect *marginalis* and *macdunnoughii* to be mutually fully fertile and so probably conspecific. This should be confirmed experimentally, if possible.

Subspecific Relationships

It will be necessary also to study sexual relations between these subspecies and adjacent ones, especially *microstriata* Comstock and *venosa* Scudder. Shapiro (*in litt.* 1979) stated that *microstriata* seemed to intergrade into *marginalis* in N. W. California. Geographic boundaries between these taxa, as well as the other adjacent "subspecies" mentioned by Eitschberger (1983), may be very uncertain (even indefinite), and it can be unsafe for us to generalize from results obtained on constituent local demes. Differences may be in part environmental (e.g. in altitude) rather than genetic. It would be desirable to re-consider the criteria for separating subspecies in this area.

Our (1981) experiments with ssp. *microstriata* were incomplete, as acknolwedged at the time, and there was a mistake in the report (p. 3, para. 5). This should read:

"One good female emerged on 20.v.79, and from this one individual all hybrid broods were derived. About 1-2 hr. after caging with a British sulphurea heterozygote *napi* male she paired with him . . . "

However the argument is little affected and the conclusions are unchanged. The female F₁ hybrids included pale yellows with the forewing underside disc pale yellow; a sulphurea allele must have been present in the white *microstriata* female used. This could be taken as suggesting at least introgression from *marginalis* or *macdunnoughii* into spp. *microstriata*, which could conflict with Eitschberger's (1983) specific separation of *venosa* and *marginalis*.

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The Mating System of Three Territorial Butterflies in Costa Rica

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Abstract. Territorial behavior was observed in three Costa Rican butterfly species whose males perch in sunspots and open areas along a forest stream. Males of *Calaenorrhinus approximatus* occupied sunspot clearings for 1-2 hr in the early morning, with the same individual defending a site for up to 19 days. Males of *Astraptes galesus cassius* perched on the broad leaves of a piper in a tree fall clearing by the stream, with one individual returning for 17 days as the territory holder. Males of *Mesosemia asa asa* perched in streamside vegetation with a maximum territorial tenure of 25 days. Territorial males of all three species regularly patrolled the area about their perching sites and responded to intruders with circling chases and ascending pursuit flights. One mating occurred in the territory of a *C. approximatus* male, and three were recorded for *M. asa* in or near a perch territory. The mating systems of these species appear convergent with other butterflies whose males defend landmark territories.

Introduction

Although there is a growing literature on butterfly mating systems (reviews by Ehrlich, 1984; Rutowski, 1982, 1984), little is known about the mating tactics of tropical butterflies. Here I describe the territorial and mate-locating behavior of two skippers (*Celaenorrhinus approximatus* Williams & Bell and *Astraptes galesus cassius* Evans) and a riodinid butterfly (*Mesosemia asa asa* Hewitson), demonstrating that these butterflies have convergently evolved a number of similarities in their mating systems. I then compare their behavior with that of a number of temperate-zone species with similar tactics.

Materials and Methods

Calaenorrhinus approximatus Williams & Bell

On the basis of two specimens, one taken outside the study period, the skippers I studied were assigned to *Celaenorrhinus approximatus*, although another very similar species, *C. eligius*, also occurs in Costa Rica (John Burrns, pers. comm.). This skipper was observed at two locations separated by about 2 km along the Rio Guacimal, a 2-3 m wide and 0.5 m deep stream that flows through lower montane wet forest at 1300 m in Monteverde, Costa Rica. The study took place from 26 April to 14 July 1986 with the observer capturing and

marking six males with Liquid Paper Typing Correction Fluid while relying on natural wing tears to identify five other individuals. I observed sites occupied by males beginning about 0800-0900. I recorded the identity of the male or males at the location over a period of several hours, while also on some days noting the number of male-male aggressive interactions, their duration, the number of patrol flights made by the male perching in the area, and the time spent in each flight.

Astraptes galesus cassius Evans

The study of this skipper took place in one of the two locations where *C. approximatus* was observed. Nine males were captured and marked with Liquid Paper during the period from 7 June to 30 July 1986. On all but 5 days I checked the perching area at intervals during the morning to record the identity of the male or males present. On some days the butterflies were observed continuously for 15 min to 1 hr in order to record the frequency of social interactions, and the duration of flights taken by the male perching at the site.

Mesosemia asa asa Hewitson

I watched this riodinid butterfly at two stream sites separated by about 150 m. I captured and marked (with Liquid Paper) eight males; five other males were identified through their distinctive patterns of wing damage. The sites were monitored from 7 June to 30 July 1986 to record which males perched there. Some days one or more males was selected for continuous observation for 15 min to 1 hr, during which time social interactions, patrol flights, and their duration were noted.

The data collected provide a picture of the daily activity pattern and the nature of territoriality of males of the three species. In addition, for two of the species, *C. approximatus* and *M. asa*, incidental observations of male-female interactions permit a description of mating behavior.

Means are presented ± 1 S.D.

Results

Daily Activity Pattern of *Celaenorrhinus approximatus*

On sunny days males flew to and perched upon leaves within sunspots 2−4 m in diameter that were located within 10 m of the Rio Guacimal. At one sunspot selected for special study between 1-14 May 1986, the first male appeared between 0801-0906 ($\bar{X}$=0834, N=10 days). At a second sunspot 2 km upstream the first male arrived between 0836-0910 (N=4 days). On overcast mornings, arrival times could be delayed until 1100.

Once have perched, usually on a broad-leaved plant less than 0.5 m from the ground, the male engaged in frequent patrol flights in which he darted about the sunspot. At both sites, resident males not only patrolled the sunspot at which they had arrived, but also occasionally visited and perched in one to three other sunspots up to 30 m distant. These patrol flights lasted from 3-32 sec ($\bar{X}$=10.4±5.7 sec; N=60 flights

by 5 males). The frequency of these flights was 1.01/min based on a total of 80 min of observations of three males on four days.

Typically males ceased flying about sunspots at some time between 0930-1030 on sunny days with the male alighting upside down under a leaf after a flight about the sunspot. Flight activity averaged 76.3 ± 18.5 min (N=7 days).

Site Tenacity and Territoriality

I identified six individuals at the same sunspots on 4 to 10 dates with a mean interval between first and last sighting of 12 ± 3.5 days. Some of the returning skippers stayed only briefly on any given day but others occupied the site for most or all of the morning activity period. These individuals, referred to hereafter as resident males, dashed after any conspecifics that flew near them. The two males would then chase one another in tight circles about the sunspot. Circle chases always preceded ascending flights, in which the two combatants flew up and away from the sunspot in near vertical flight into the forest canopy. Some interactions consisted of a series of circle and ascending flights, with the two rivals descending separately after an ascent and returning to the sunspot to repeat the cycle anew.

The frequency of aerial fights was 9.5/hr (N=10.9 hrs of observation). The mean duration of these contests was 46.4 ± 42.0 sec (N=34 fights recorded on 11 days). Intraspecific chases lasted much longer on average than either patrol flights ($\bar{X}=10.4$ sec, see above), or flights triggered by other passing butterflies, tachinid flies and damselflies ($\bar{X}=4.7 \pm 2.1$ sec, N=24 chases recorded on 4 days).

In 66 of 85 fights, only one male returned to perch in the sunspot after a circle flight or ascending flight. In 63 of 66 cases, the sole returning male was the resident male who had occupied the site first that day. When two males did land in the same sunspot after an aerial chase, it was generally only a matter of a minute or two before one male patrolled the sunspot eliciting a new chase and (usually) the departure of the newcomer.

Ousters of territory-defending males were observed three times. On 1 May an unmarked male with fresh undamaged wings displaced *yellow* after a long series of aerial chases. Twice males that had been residents on preceding days arrived late at their sunspot to find the site occupied by another male; in both cases turnovers occurred, with the previous day's resident quickly ejecting the newcomer.

Thus the general pattern was for one male of claim a perch site for all of the morning activity period over several days. Other males, including previous residents, might visit the site over a number of days but they did not remain long.

Male-Female Interactions

I saw one copulation in about 20 hr of observation. This mating was discovered after its inception when I noticed that the resident male was

no longer perhcing in his sunspot. In his place was an unmarked individual. The resident was under a broad leaf within his territory copulating with an apparently fresh female with unworn wings. If the mating occurred at about the time when the resident disappeared from view, the duration of copulation would be about 1 hr.

Daily Activity Pattern of *Astraptes galesus cassius*

Males of *A. g. cassius* came in the morning to a stand of broad-leaved *Piper auritum* (Piperaceae) growing at the edge of the Rio Guacimal. On six sunny mornings between 7 June and 13 July, the first male to perch on an exposed piper leaf appeared before 0830 (0808 was the earliest record). On cloudy days arrivals were delayed, but one or more males perched on the piper for at least brief periods on 30 of 36 days during the study, even if the sun did not shine. Activity ceased in steady rain but otherwise males remained at the site until some time between 1100-1200 (the latest record was 1157). Thus males were active 2-3 hr per day.

The leaves used as perches were 2-3 m above the ground with the primary perch site situated in the middle of a large (roughly 15 m diameter) clearing created by tree falls. The piper received direct sunlight only for a short period during the latter part of the morning. Perching males often flew out from and returned in a few seconds to the same leaf. Longer (10-20 m) patrol flights along the stream course lasted from 4 to 25 sec with a mean of 10.2 ± 4.2 sec ($N = 79$ flights of 5 males on 7 days). The frequency of patrol flights was 39.3/hr (4.5 hr of observations of 4 different males on 8 dates).

Site Tenacity and Territoriality

Marked individuals often returned to the piper patch over many days and stayed for several hours each morning (Table 1). The resident male chased intruders in straight horizontal pursuits and ascending flights that were not as structured as the circle/ascending flights of *C. approximatus*. Visitors usually left the area quickly when pursued. Male-male interactions occurred an average of 16.6 per hr ($N = 5.5$ hr observation of 4 residents). Chases of conspecifics lasted an average of 25.3 ± 12.6 sec ($N = 39$).

A change in territory ownership occurred on 7 occasions (Table 1) during 52 days. The new males all had less damaged wings than the old residents that they replaced after a number of chases. Previous residents continued to return to the site on subsequent days in 4 cases (Table 1), often coming earlier than their replacements. For example, on 24 June, *green* occupied the central piper plant from 0919-0952, giving way only when *yellow* finally arrived (*yellow* having claimed the territory on 16 June). Although past residents were always quickly displaced by the new owner, at least one male (*yellow*) succeeded in reclaiming the site

Table 1. Identified males of *Astraptes galesus cassius* at one site from 7 June to 28 July 1986. R=resident territory owner, v=non-territorial visitor, R*=males loses territory to rival.

Male	June 7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
pink	R----R*				v					v					v		
green		R	----	----	----	----	----	----	----	R*	v	v	v	v			
yellow o/o										R	----	----	----	----	----	----	----

	June 24	25	26	27	28	29	30	July 1	2	3	4	5	6	7	8	9	10	11
pink	v																	
green	R*	v	v	v	v			v	v	v								
yellow o/o	R---R*		v	v		R	----	----	----	----	----	----	----	----	----	----	----	----
blue		R	----	----R														

	July 12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
pink																	
green																	
yellow o/o	R*	v															
blue																	
wing mark	R	----	----	----	R*												
yellow ii					R	----	----	----	----	R*							
wing notch										R	----	----	----	----	----	----	----

for 12 more days (Table 1) when the male that had defeated him failed to reappear on 30 June.

Daily Activity Period of *Mesosemia asa asa*

Males arrived at their streamside perches between 0930-1030 (N=12 days) and they departed on sunny afternoons between 1400-1500 (N=3 days) with one record of a male present until 1516. The butterflies perched on exposed leaves 0.5 to 1.5 m above the ground, and they faced out into the open space created by the stream channel. Early in the morning males often selected sites that were in full sun, but they were active even when all perches were shaded.

During 6 hr of watching five males, I recorded 14.3 perch shifting flights of 1-3 sec per hr. Longer patrol flights of 3 m or more lasting on average 9.1 ± 4.6 sec (N=14) occurred at the rate of just 3.8 per hr during this same period.

Territorial Behavior

Along a 150 m stretch of stream there were only four perching sites,

one downstream at a bend in the Rio Guacimal, and three 10-15 m apart at an upstream bend near the piper stand occupied by males of *A. g. cassius*. The relatively open forest canopy at these places permitted the sun to penetrate to a greater degree than elsewhere.

Marked males often returned to the same perch location day after day (Table 2), chasing away intruders in slow circling flights, or occasionally slow ascending flights, a series of which might last as long as 4 min. Intraspecific aerial interactions occurred at the rate of just 5/hr based on 8 hr of observation. The mean duration of these interactions was 24.7 ± 25.1 sec (N=48 chases). Interspecific chases of certain other butterflies lasted on average 5.9 ± 4.4 sec (N = 51 chases).

Turnovers in territory ownership took place six times during 43 days at three different perch sites (Table 2). The most dramatic of these occurred at a perch site that had been occupied for 25 days by a male that had lost the tip of one forewing. On 12 July an unusually large, fresh male with no wing damage displaced the resident from a perch site next to clipped wing's territory. The next day the large male moved into clipped wing's territory and engaged him in at least 16 aerial chases. Clipped wing left the site but continued to return at intervals on this and the next day, each time being chased off by the newcomer.

Male-Female Interactions

Three matings of *M. asa* were observed at 1138 on 8 June, 1205 on 24 June, and 1248 on 21 July. All occurred when a female flew into a territory and was pursued by the resident male. The female then landed

Table 2. Territorial males of *Mesosemia asa* at four territories observed from 18 June to 30 July. Note shifts between territories 1 and 2 by male B.

	June 18 19 20 21 22 23 24 25 26 27 28 29 30 July 1 2 3 4 5 6 7 8
Territory	
T1	Male A --
T2	Male B -------------------------------------
T3	Male C --
T4	Male D --

	July 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
T1	Male A-----------B ------------------- E F -----------------------G------------H-------
T2	Male B-----------I ------- B--
T3	Male C-----------------I---
T4	Male D

on the underside of a leaf with the male alighting beside her. Copulation followed quickly with minimal courtship; "T_f" (Burns, 1970) was exactly 52 min in one case, while copulation lasted between 40-75 min in the two other cases.

Discussion

Table 3 provides a summary of male behavior in the three butterflies. There are both differences and similarities in the mating system of these unrelated species. The butterflies differ in the timing and duration of their daily mate-locating activity, but each species is active for only a fraction of each day. All three species perch in relatively open areas, with *Celaenorrhinus* especially dependent on sunspots. These areas are not only relatively free from visual obstruction so that males may detect passing females, but may also offer thermoregulatory advantages in cool rainforest habitats. Males of the two skippers patrol their territories often, whereas the riodinid *M. asa* flies from perches infrequently. Territorial males of all three species engage intruders in ascending flights (although speed of flight varies greatly among species). Residents are able to control their perching areas up to two weeks or more, but they encounter receptive females at very low frequency.

Callaghan (1982(83)) has documented similar behavior in a number of other tropical riodinids whose males wait on perches along the very edge of forests or in treefall areas; Scott (1974, 1975, 1982) has observed some North American skippers in which male mate-locating activity is concentrated in gulches and ravine bottoms. In these cases, males appear to take advantage of natural features that channel females past certain points. Similarly, hilltopping species (Shields, 1967; Scott, 1970), seem to be making use of conspicuous topographic features that may guide the movements of females. Landmark-based mating systems

Table 3.   A comparison of the mating system of two territorial streamside skippers, *Celaenorrhinus approximatus* and *Astraptes galesus*, and the riodinid butterfly, *Mesosemia asa*.

	C. approximatus	A. galesus	M. asa
Activity period	< 2 hr 0830-1030	ca. 3 hr 0830-1130	ca. 4 hr 1000-1400
Patrol flights - frequency: mean duration	60/hr: 10 sec	39/hr: 10 sec	3.8/hr: 9 sec
Fights-frequency: mean duration	9.5/hr: 46 sec	16.6/hr: 25 sec	5.5/hr: 25 sec
Observed matings	1	0	3
Maximum territorial tenure	19 days	21 days	25 days

apparently evolve when males cannot profitably search for mates at larval foodplants or adult nectar sources (Thornhill and Alcock, 1983).

Territoriality is widespread in the landmark and sunspot mating system group (e.g. Shields, 1976; Davies, 1978; Bitzer & Shaw, 1979(80); Callaghan, 1982(83); Lederhouse, 1982; Wickman & Wicklund, 1983; Alcock, 1983, 1985; Alcock & O'Neill, 1986). Males typically compete for landmark territories with elaborate circling and vertical ascending flights (see also MacNeill, 1964). These interactions appear to involve demonstrations of speed and aerial agility to rivals, as well as endurance in those cases in which repeated vertical pursuit flights occur.

Convergent evolution is also evident in the behavior of females of this group, which fly toward perched males, leading them on a slower, more direct pursuit flight than that seen in male-male fights. Females that are receptive alight quickly, and males land beside them to offer only the briefest of courtships before copulation occurs (e.g. Alcock, 1985; Alcock & Gwynne, in press; Wickman & Wiklund, 1983).

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Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest

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Abstract. 1) Paired traps showed that fruit-feeding nymphalid butterflies in the subfamilies Nymphalinae, Charaxinae, Morphinae and Satyrinae are stratified between the canopy and the understory by species composition, and abundance, size, and color pattern. 2) Short wing lengths and uniform underside patterns are found in the canopy, whereas long wing lengths and underside patterns bearing eyespots are found in the understory. 3) Wing length and color pattern cannot be separated from taxonomic affinity, and hence, these butterflies stratify by subfamily: Charaxinae and Nymphalinae in the canopy, Morphinae and Satyrinae in the understory. 4) A general model is presented to explain the apparent breakdown of stratification along forest edges and how light levels act as barriers to maintain insect stratification.

Introduction

The tropical rainforest has been described in terms of component layers or strata (Richards, 1966), and stratification (i.e. vertical distribution) of rainforest organisms has been documented for mammals and birds (Allee, 1926; Dunn et al., 1968; Orians, 1969; Pearson, 1971), and for insects (Bates, 1944, 1947; Corbet, 1961a & b; Davis, 1944; Elton, 1973, 1975; Erwin, 1983; Erwin & Scott, 1980; Garnham et al., 1946; Galino et al., 1951; Haddow, 1945; Haddow & Corbet, 1961a; Jackson, 1961; Papageorgies, 1975; Pittendrigh, 1950a & b; Rees, 1984; Snow, 1955; Sutton, 1979, 1984; Sutton & Hudson, 1980; Wolda, 1979). Studies on the stratification of insects other than mosquitos range from general overviews of all insect taxa taken in a sample (Elton, 1973; Sutton, 1984; Sutton & Hudson, 1980) to comments on a few taxa within a sample (Corbet, 1961b; Erwin, 1984; Erwin & Scott, 1980; Jackson, 1961; Papageorgis, 1975; Rees, 1984; Wolda, 1979). Of these studies, only two have attempted to quantify the stratification of butterflies. Jackson (1961) documented the presence of rare Lycaenidae and Nymphalidae in a Ugandan forest canopy, but his study ignored all species in the understory. In Peruvian lowland rainforest, Papageorgis (1975) found that some warningly colored butterflies and diurnal moths tend to fly at different levels in the forest according to mimetic pattern.

Excluding those species where males visit wet sand or plant material for non-nutritional resources (see Boppré, 1984; Collenette & Talbot, 1926; Norris, 1936), any tropical forest community of butterflies can be divided into two adult feeding guilds: those species that obtain the bulk of their nutritional requirements from flower nectar (all Papilionidae, Pieridae, Lycaenidae, Riodinidae and some Nymphalidae), and those species that feed upon the juices of rotting fruits, fermenting sap, or animal waste (several subfamilies of the Nymphalidae (sensu Ehrlich, 1958)). In the neotropics, only the members of the nymphalid sub-families Satyrinae, Morphinae, Charaxinae, and some members of the Nymphalinae feed exclusively on rotting fruits or other non-floral liquid as adults. These latter subfamilies, hereafter referred to as "fruit-feeding nymphalids," may account for over 50% of the nymphalid species diversity in some Central American habitats and can, in general, only be collected by baiting them with rotting fruits (DeVries, 1987).

By virtue of their feeding habits, fruit-feeding nymphalids may be used to study stratification because individuals can be selectively sampled with traps. In this paper I present quantitative evidence for several patterns of stratification among these butterflies from a Costa Rican rainforest, and discuss how forest structure may effect stratification.

Methods

The study was conducted from 20 October 1979 through 2 January 1980 at Finca La Selva, Heredia Province, Costa Rica, within the area known locally as the 'Washington Plots.' Five trapping sites (see trap design in DeVries, 1987) within closed canopy forest, each of which had an emergent canopy tree with a small lightgap at its base, were chosen on the basis of their receiving at least one hour of direct sunlight each day. The entire study was done during the rainy season, a time when butterfly abundance is low.

One trap of each pair was placed in the canopy, the other in a small lightgap immediately below it. Canopy traps were positioned by fastening a pulley to a tree limb growing over a lightgap and using a rope to raise and lower the trap from ground level. Traps were checked twice each day, and rotting banana bait replaced regularly. All butterflies caught in the traps were killed, measured (winglength), and determined to species and sex and the trap position of capture was noted. Winglength data (measured from base of forewing to the forewing apex) were supplemented for species with small sample sizes using Costa Rican specimens from the Museo Nacional or British Museum (Nat. Hist.) collections (Table 3); these data were log transformed for analysis. The nomenclature used here follows DeVries (1987), and for analyses the subfamily (Table 2) Brassolinae was collapsed into the Morphinae of Ehrlich (1958).

Results: Patterns of Stratification

The wet season depression of butterfly abundance is reflected by the low numbers of individuals trapped: in 10 weeks the traps collected a total of

182 butterflies in 46 species (Table 1). As one might expect, some rare species (based on museum abundance) were common in the canopy, and in all categories (by subfamily and trap position) significantly more (DF = 4; G = 49.1; p < .001, DF = 1; G = 42.3; p < .001 respectively) males were caught than females (Table 1). The trap samples also contained previously undescribed taxa (see Singer et al. 1983; DeVries 1987). Without addressing the problems of trap effect, heterogeneity of trap catch, or the possible effects of sampling without replacement, these overall patterns were noted:

1. Most species tended to be trapped only in the canopy or the understory, but a few species were found in both (Table 1).

2. Species richness was about the same in canopy and understory, with 24 taxa trapped only in the canopy, 15 only in the understory, and 7 taxa in both (Table 1).

3. Canopy taps collected significantly more individuals than did understory traps (Table 1).

4. Stratification occurred at the subfamily level, with members of the Charaxinae and Nymphalinae in the canopy, and members of the Morphinae and Satyrinae in the understory (Table 2).

5. Species trapped in the canopy had smaller mean winglengths than those species trapped in the understory (Table 3).

6. Mean winglengths differ between subfamilies, implying that winglength and position of capture cannot be separated from phylogenetic affinity (Table 3).

7. Canopy and understory butterflies differ in possession of eyespot patterns (Table 4), and these differences are linked to taxonomic affiliation: Morphinae and Satyrinae have eyespots while other groups generally do not.

Discussion

This study showed that certain genera and species of fruit-feeding nymphalid butterflies were trapped consistently in the canopy, others in the understory, while a small fraction of the species were found in both canopy and understory. Overall, the data here indicate differences between canopy and understory butterflies in abundance, species composition, wing length, and color pattern (Tables 1-4). However, the stratification of butterfly species by wing length and color pattern cannot be separated from taxonomic relatedness. This is to say that position of capture, size, color pattern, and subfamily are correlated to some degree, and that similar patterns may be found in other arthropods.

The winglength data presented here are consonant with size data from other arthropod studies (Wolda 1979; Erwin & Scott 1980; Rees 1982; Erwin 1983), suggesting that smaller relative size may be a general characteristic of canopy insects. This trend, however, is reversed

for Costa Rican Papilionidae, where larger winged butterflies occur in the canopy (DeVries, unpublished data).

Stratification by color pattern in fruit-feeding nymphalids is not likely to be explained by the mimetic resemblance hypothesis of Papageorgis (1975) *per se*. In her system, predators maintain the stratification of butterflies by selecting for similar mimetic patterns within distinct strata. However, virtually all of the species in the present study are cryptically colored, palatable to predators, and non-mimetic (Chai 1986; DeVries 1987). Since predators are clearly important in selecting the appearance of cryptic insects (Kettlewell 1955, 1956; Chai 1986), the stratification of eyespots (or lack of them) found in this study may also be due to stratification patterns of the butterflies' predators. It is quite reasonable to assume that the species composition of vertebrate predators (i.e., lizards and birds) differs between the canopy and understory, and that these predators exert differing selection pressures on butterflies. Perhaps studies on a single subfamily that contains species found in both canopy and in the understory (e.g., Nymphalinae or Satyrinae) may prove fruitful for probing the effects of how predator communities in the canopy and understory act on eyespot pattern (and body size) of these cryptic butterflies.

Although the data here show that fruit-feeding nymphalid species are stratified between canopy and understory when feeding, they do not necessarily indicate where these butterflies spend their time when not feeding. For instance, the males of some species trapped only in the understory (*Archaeoprepona camilla, Morpho cypris*) spend much of their time patrolling in the canopy (presumably searching for females), and conversely, females of some rarer canopy species (*Cissia pseudo-confusa, Megeuptychia antonoe, Catonephele orites*) are known to oviposit on hostplants occurring near ground level in gaps and along forest edges (DeVries 1986; 1987). Clearly, the location of mate seeking areas or larval hostplants can be entirely different from where non-ovipositing adults are found. Furthermore, these data here do not indicate whether or not further stratification would be revealed if traps had been placed at intermediate levels between the canopy and understory. The data do, however, raise the question of why these butterflies show pronounced stratification: if Newton was correct about apples, rotting fruits fall to the ground and canopy butterflies should feed on them there. This suggests that fruit-feeding nymphalids may eventually be shown to have feeding specializations with respect to rainforest fruit species.

Most tropical collectors are aware that canopy flying nymphalids can be trapped close to ground level along a forest edge. Such knowledge implies an intuitive appreciation that stratification breaks down in some situations. A testable, general model is offered here to explain how different light levels maintain the stratification observed in fruit-feeding nymphalids, and why stratification is less pronounced in certain habitats. The model assumes that for diurnal insects such as butterflies,

Table 1.   Summary of taxa trapped during the study. See DeVries (1987) for
           nomenclatural details.

Species	Canopy	Understory	Total
CHARAXINAE			
Prepona			
omphale	6	1	7
Agrias			
amydon	1	0	1
Archaeoprepona			
demophon	2	1	3
camilla	1	4	5
meander	0	1	1
Zaretis			
itys	1	0	1
Memphis			
morvus	5	0	5
cleomestra	3	0	3
laura	1	0	1
aureola	1	0	1
xenocles	3	0	3
NYMPHALINAE			
Hamadryas			
laodamia	21	0	21
arinome	16	2	18
amphinome	3	0	3
Catonephele			
numilia	4	0	4
orites	11	0	11
Nessaea			
aglaura	1	4	5
Myscelia			
leucocyana	5	3	8
cyaniris	1	0	1
Eunica			
monima	1	0	1
Callicore			
lyca	1	0	1
patelina	2	0	2
Historis			
odius	3	0	3
acheronta	3	0	3
Smyrna			
blomfildia	3	0	3
Colobura			
dirce	8	0	8
Tigridia			
acesta	2	2	4

Table 1.   (cont'd)

Species	Canopy	Understory	Total
MORPHINAE			
Morpho			
peleides	0	1	1
amathonte	0	1	1
cypris	0	1	1
Antirrhea			
miltiades	0	1	1
Caligo			
eurilochus	0	4	4
atreus	0	9	9
illioneus	0	2	2
Catoblepia			
orgetorix	0	1	1
Opsiphanes			
tamarindi	0	1	1
invirae	2	0	2
cassinae	2	0	2
SATYRINAE			
Cithaerias			
menander	0	2	2
Dulcedo			
polita	0	1	1
Cissia			
pseudoconfusa	3	0	3
joycae	1	0	1
hesione	0	3	3
Megeuptychia			
antonoe	11	0	11
Taygetis			
Andromeda	0	5	5
xenana	1	3	4
Total	129	53	182

Subfamily	male-female canopy	male-female understory	Total
Charaxinae	19:5	5:2	31
Nymphalinae	59:26	7:4	96
Morphinae	2:2	15:6	25
Satyrinae	13:3	14:0	30
Total	129	53	182

Table 2. Abundance of individuals by subfamily and position of traps. Expected
          values are in parentheses. Significantly more butterflies were trapped
          in the canopy than the understory [DF = 3; G = 54.67; p. < .0001].

Subfamily	Canopy	Understory	Total
Charaxinae	24 (21.97)	7 (9.03)	31
Nymphalinae	85 (68.04)	11 (27.96)	96
Morphinae	4 (17.72)	21 (7.28)	25
Satyrinae	16 (21.26)	14 (8.74)	30
Total	129	53	182

Table 3. Mean Winglengths based on Costa Rican Specimens

Species	N =	Winglength	Subfamily	Position
omphale	7	48.4	charax	both
demophon	9	55.5	charax	both
camilla	6	59.5	charax	both
meander	8	53.7	charax	under
itys	7	35.1	charax	canopy
morvus	8	32.4	charax	canopy
cleomestra	12	32.8	charax	canopy
aureola	7	35.4	charax	canopy
xenocles	7	29.5	charax	canopy
laodamia	8	35.0	nymph	canopy
arinome	8	37.0	nymph	both
amphinome	9	37.7	nymph	canopy
numilia	7	36.2	nymph	canopy
orites	8	34.1	nymph	canopy
aglaura	8	35.9	nymph	both
leucocyana	9	29.3	nymph	both
cyaniris	10	34.1	nymph	canopy
monima	10	21.8	nymph	canopy
lyca	10	25.7	nymph	canopy
patelina	8	28.7	nymph	canopy
odius	8	56.0	nymph	canopy
acheronta	5	44.0	nymph	canopy
blomfildia	8	41.2	nymph	canopy
dirce	7	32.5	nymph	canopy
acesta	10	25.7	nymph	both
peleides	12	71.3	morph	under
amathonte	10	78.1	morph	under
cypris	8	70.0	morph	under
miltiades	9	47.3	morph	under
eurilochus	9	81.6	morph	under
atreus	8	77.7	morph	under

Table 3.   (cont'd)

Species	N =	Winglength	Subfamily	Position
illioneus	6	69.9	morph	under
orgetorix	10	51.8	morph	under
tamarindi	13	48.9	morph	under
invirae	8	43.0	morph	canopy
cassinae	11	42.0	morph	canopy
menander	10	30.3	satyr	under
polita	6	34.4	satyr	under
pseudoconfusa	8	20.9	satyr	canopy
hesione	7	20.8	satyr	under
antonoe	7	31.9	satyr	canopy
andromeda	8	37.0	satyr	under
xenana	9	36.4	satyr	under

One Factor ANOVA on Winglength across trap position and subfamily.

Source	S.S.	DF	Mean sq.	F-test	
between traps	1.343	2	0.672	6.716	
within traps	4.000	40	0.100		$p < .005$
Total	5.344	42			
between subfams	2.935	3	0.978	15.84	
within subfams	2.409	39	0.062		$p < .0001$
Total	5.344	42			

Table 4.   Stratification of species by presence or absence of eyespot pattern. Expected values are in parentheses. Eyespot patterns are found with a significantly greater frequency in the understory than in the canopy (DF = 1; G = 25.23; p = .0001). Note that this cannot be separated from taxonomic affinity: Morphinae and Satyrinae have eyespots.

Eyespots	Canopy	Understory	Both	Total
Present	5 (9.39)	13 (5.87)	0 (2.74)	18
Absent	19 (14.61)	2 (9.13)	7 (4.26)	28
Total	24	15	7	46

light is more important than the related factors of temperature and humidity for explaining patterns of stratification. The model therefore predicts that: 1) butterfly taxa usually fly in certain light levels within any habitat, and that 2) drastic changes in light intensity act as barriers between habitats.

The flower-feeding butterflies *Anartia fatima* (Nymphalidae), *Phoebis philea* (Pieridae), *Battus polydamas* (Papilionidae) that usually fly in bright sun, at ground level, provide an illustration of the effects of a light barrier. I commonly see these butterflies fly across a pasture towards the forest edge, ascend at the forest edge, fly across the canopy, and descend once again to ground level when the next pasture is encountered. They do not move through the shade of the forest, but rather they treat the canopy as an elevated pasture, despite the 40 meter difference in height beween canopy and ground levels. In this example, a butterfly changes vertical distance from the ground without experiencing an appreciable change in light intensity. I strongly suspect that butterfly species that inhabit the vegetational interface between sunny and shaded areas (i.e., canopy/edge) treat the forest canopy and forest edge without regard to vertical position, since light levels within the interface should remain roughly the same regardless of height.

Stratification then, in both canopy and pasture species is probably maintained by their preference for certain light levels. From field observations I further reason that there are three major distribution zones for butterflies within a closed canopy forest: open areas above and around the canopy (high light levels), the combination of within canopy and forest edge (medium light levels), and the shade of the forest interior (low light levels). Canopy species can be trapped at ground level at the forest edge because they normally inhabit the light level interface between bright sunlight and deep shade, and like vining plants, treat the forest edge as the canopy come to the ground. Light is considered to be an important factor in maintaining stratification in some forest and marine communities (Bainbridge et al. 1966; Allee et al. 1969), yet the effect the forest edge or disturbed forests have on stratification has not been addressed in tropical forest insects. If differences in light levels are important for maintaining stratification in rainforest butterflies, we might predict that in habitats without pronounced differences in light levels (i.e., disturbed forest, in deciduous forest during the dry season, or along the forest edge), stratification will not be as distinct as in closed canopy forest. The study of fruit-feeding nymphalids across various forest successional stages with the methods described herein may provide the necessary tools for understanding the role of light levels and forest structure in the maintainence of stratification of rainforest butterflies.

and the University of Texas at Austin. This paper is dedicated to the stratified diversity of Clifford Brown, Horace Silver, and Art Blakey.

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Euphydryas anicia and *E. chalcedona* in Idaho (Lepidoptera: Nymphalidae)[1]

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Abstract. The nymphalid species *Euphydryas anicia* and *E. chalcedona* are sympatric in several areas in Idaho and easily separated from one another by features of the male genitalia and differences in forewing maculation. While *anicia* and *chalcedona* are closely related, distinct differences can be identified, thus substantiating their separation as two species.

Introduction

The taxa *Euphydryas anicia* (Doubleday) and *E. chalcedona* (Doubleday) have been considered historically to represent separate species, and they have been so treated in the two most recent lists of the North American butterflies (Miller & Brown, 1981; Hodges *et al.*, 1983), as well as in two recent papers (Brussard *et al.*, 1985; Spomer & Reiser, 1985). Based upon his analysis of the male genitalia of these insects, Scott (1978[80]) considered these two taxa conspecific. My field studies in Idaho indicate that *E. anicia* and *chalcedona* occur sympatrically at several localities, and that they may be separated on the basis of characters in the male genitalia and dorsal wing maculation.

Following the findings of Brussard *et al.* (1985), the generic name *Euphydryas* is used in this paper rather than *Occidryas* Higgins.

Study Areas

Fig. 1 is a map showing the distributions of *Euphydryas anicia* and *E. chalcedona* in Idaho. The records are based on my own collecting and data provided by Stanford (1985). Both species occur widely in Idaho, but to date they have been found to be truly sympatric in two localities only. The first site is in Boundary Co. and lies east of Hwy. 95 and northwest of Moyie Springs in the Kaniksu National Forest. Both *E. anicia* and *E. chalcedona* were collected on July 6–7, 1985 flying together in a small open meadow near a railroad right-of-way.

The second site is in the Bear Valley region of Valley Co. in the
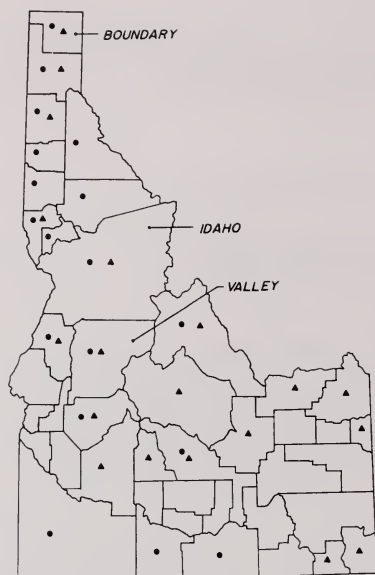
Fig. 1 Idaho map showing distribu-
        tion by county of *E. anicia*
        (triangles) and *E. chalcedona*
        (solid circles).

vicinity of the Deer Creek crossing of the Boise National Forest road
that connects Warm Lake with Hwy. 12. Specimens of the two species
were taken together along the road and on an adjoining cleared forest
slope on July 24, 1984. Elsewhere in Valley Co., *chalcedona* occurs in
the Payette National Forest just north of McCall, and *anicia* is found in
the general vicinity of Warm Lake and Stolle Meadow.

Study Material

  During this study, 283 Idaho specimens (106 *anicia*, 175 *chalcedona*, 2
equivocal) were examined.

Wing Maculation

  Euphydryas chalcedona throughout its range in Idaho is relatively
constant in facies. Adults are dorsally predominately black with red-
and-white maculation; ventrally the ground color is brick red. The
subspecific epithet usually applied is *wallacensis* Gunder (= *huelle-
manni* dos Passos). Two typical pairs are shown in Fig. 2.
  Euphydryas anicia in Idaho is variable. In the broad sense, it can be
divided into two color groups: 1. dorsal ground color generally black; 2.
dorsal ground color red/orange. Both forms manifest pale white or
cream-colored spots dorsally. The dark form displays red markings
similar to those of *chalcedona*. The ventral ground color of Idaho *anicia*
varies from brick red to red-orange. The VHW pale intercellular
maculation varies in extent according to local colony. Because of the
variability of *anicia* in Idaho, no subspecific epithets are applied in this
paper.
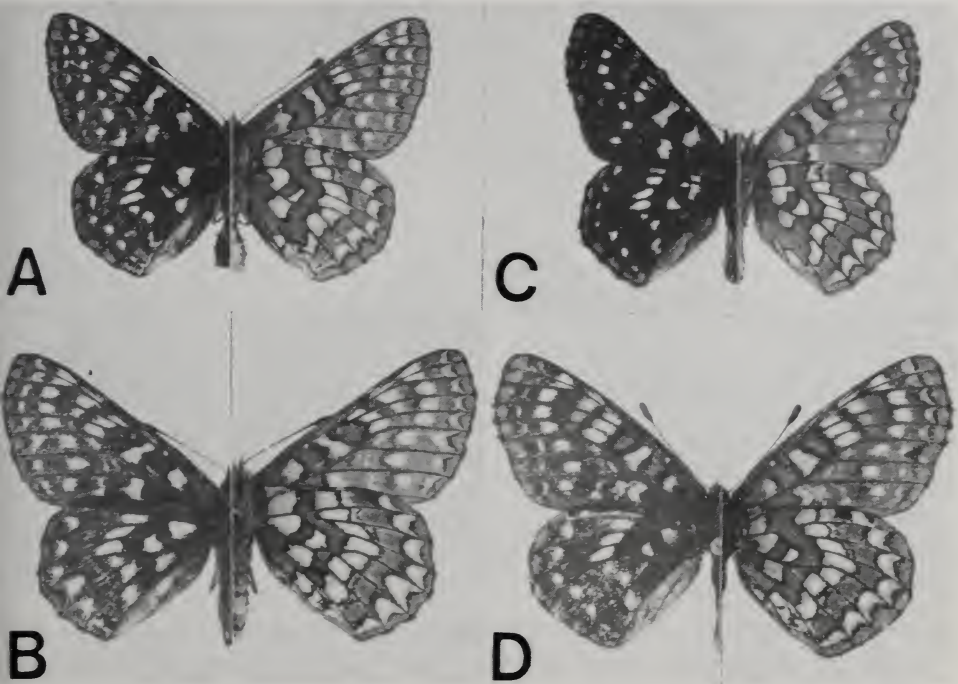
Fig. 2. *E. chalcedona wallacensis* from Idaho. Dorsal surfaces left; ventral right. A. Male. Payette Nat. For., 1 mi. N. McCall, Valley Co., 1.vii.83. B. Female. Same locality, 13.vii.84. C. Male. Canyon Creek, Idaho Co., 31.v.85. D. Female. Kaniksu Nat. For. NW Moyie Springs, Boundary Co., 7.vii.85. All C. D. Ferris Coll.

Specimens of *anicia* collected at the Boundary Co. site are brightly colored and belong to the red/orange category. Two color forms of *anicia* occur in Valley Co.: 1. a red form similar to the Boundary Co. phenotype, but not so brightly colored; 2. specimens that generally fall into the black category, but variable.

Some of the dark *anicia* specimens appear in maculation superficially similar to *chalcedona*. These two species can be separated, however, on the basis of the form of the marginal spot-band on the DFW, as illustrated in Fig. 3. In both sexes of *anicia*, the DFW marginal spots form a complete border along the outer edge of the wing. In *chalcedona wallacensis*, the spot-row normally terminates about vein Cu_1 in the males, and although it frequently extends to vein 2A in the females, the spots are much reduced in size below vein Cu_1. This spot-row in *anicia* is clearly double at the apex of the FW, while in *chalcedona* immediately basad of the marginal red spot-row, there is a blackish band distad of a row of small whitish spots. The apical double spot-row in *anicia* may present concolorous spots, or the inner row may contain whitish spots. Ventrally, especially on the HW, *chalcedona* generally
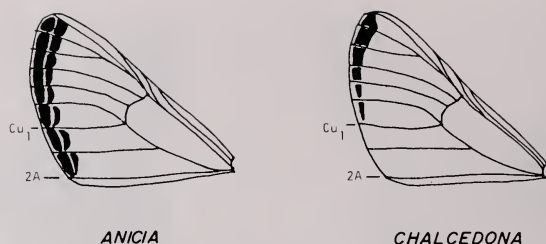
ANICIA   CHALCEDONA

Fig. 3.   DFW marginal spot-band maculation in Idaho *E. anicia* and *chalcedo-na.*

displays much more extensive brick-red coloration than is found in *anicia*, but this character is not relaible. Fig. 4 depicts specimens of *E. anicia* from the Boundary Co. (A-B) and Valley Co. (C-D) populations. Fig. 5 illustrates a pair of the dark phenotype from Stolle Meadow in Valley Co.

Genitalic Studies

Fig. 6 depicts the diagnostic portions of the male genitalia of *E. anicia* and *E. chalcedona* from Idaho. In this figure, drawings A and E represent typical *chalcedona*, while B-D and F represent typical *anicia* (G will be addressed subsequently). These illustrations show the distal portion of the right valve and its processes with the abdomen rotated 90° from normal life position. This is the view of the genitalia seen using a binocular dissection microscope after the abdominal hairs have been removed (by use of a stiff brush). It is not necessary to dissect the genitalia from the abdomen. To achieve the views shown in Fig. 6, it may be necessary to angle the specimen relative to the microscope objective.

As the illustrations show, *E. chalcedona* manifests one long and curved process, and a short pointed process (which may be slightly recurved). By contrast, *anicia* presents two long curved processes (frequently of nearly equal length) which various authors have likened to knitting needles. In my studies of males of *anicia* collected from Chihuahua, Mexico to the southern Yukon Territory, the valvular processes are remarkably consistent in form, and do not intergrade into the form found in *chalcedona*. The two species, however, may hybridize as discussed below.

Intermediate Specimens

Of the Idaho material, only one pair of intermediate specimens has been found. They are illustrated in Fig. 7, with male genitalia in Fig. 6 (G). In dorsal maculation, both specimens are closer to *chalcedona* than *anicia*, although the form of the male genitalia is closer to *anicia*. This pair may represent a hybrid between the two species, but more likely it
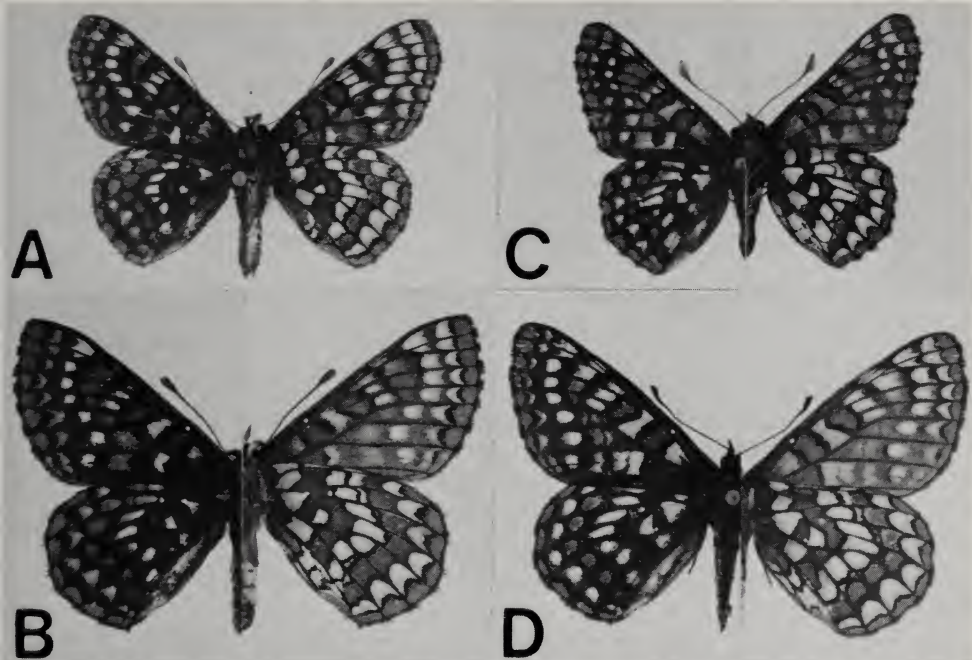
Fig. 4. *E. anicia* from Idaho. Dorsal surfaces left; ventral right. A. Male, red/orange form. Kaniksu Nat. For. NW Moyie Springs, Boundary Co., 6.vii.85. B. Female. Same data. C. Male, red/orange form. Deer Creek, Boise Nat. For., Valley Co., 24.vii.84. D. Female. Same data. All C. D. Ferris Coll.
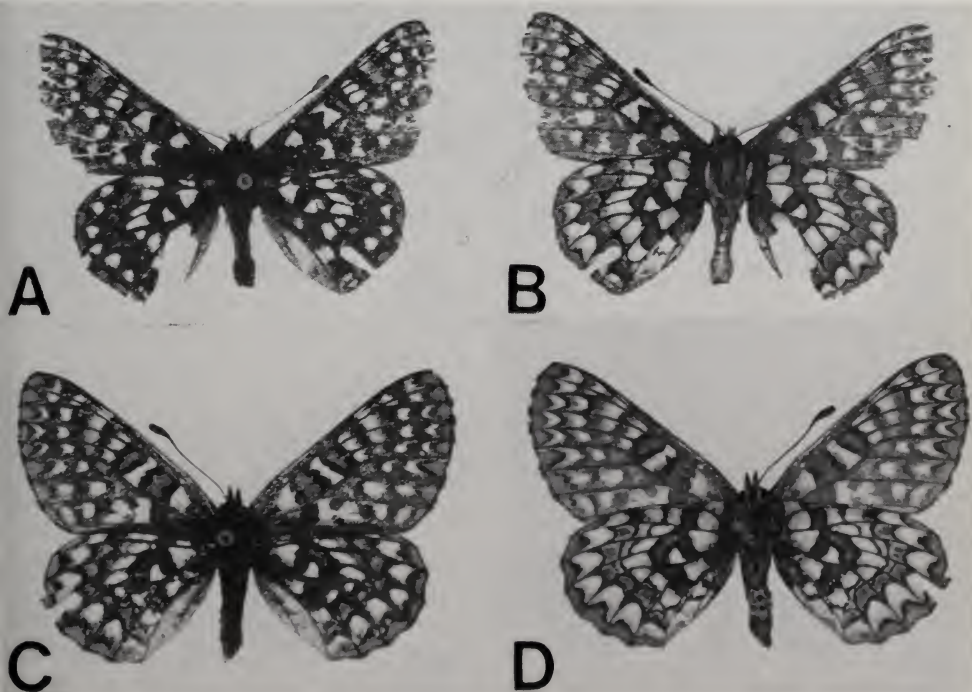
Fig. 5. *E. anicia* dark form from Stolle Meadow, Boise Nat. For., Valley Co., Idaho, 13–17.vii.83. A. Male, dorsal. B. Male, ventral. C. Female, dorsal. D. Female, ventral. All C. D. Ferris Coll.
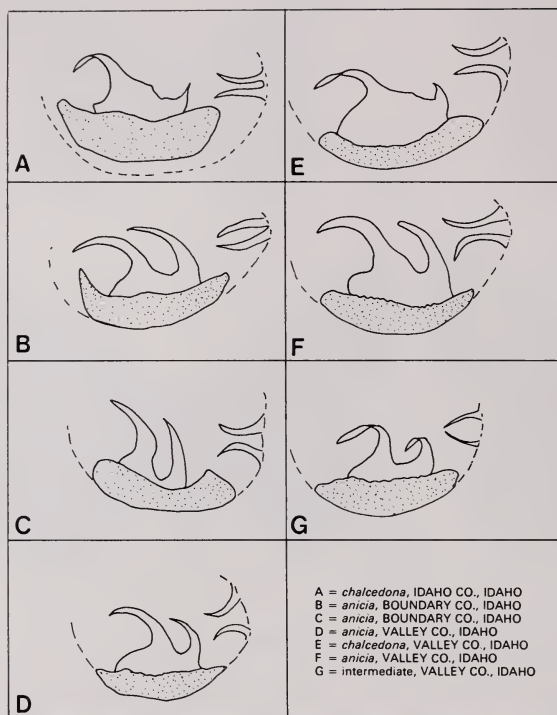
Fig. 6   Male genitalia (valvular processes) of Idaho *Euphydryas*. A, E. *E. chalcedona*. B–D, F. *E. anicia*. G. Equivocal specimen.

A = *chalcedona*, IDAHO CO., IDAHO
B = *anicia*, BOUNDARY CO., IDAHO
C = *anicia*, BOUNDARY CO., IDAHO
D = *anicia*, VALLEY CO., IDAHO
E = *chalcedona*, VALLEY CO., IDAHO
F = *anicia*, VALLEY CO., IDAHO
G = intermediate, VALLEY CO., IDAHO
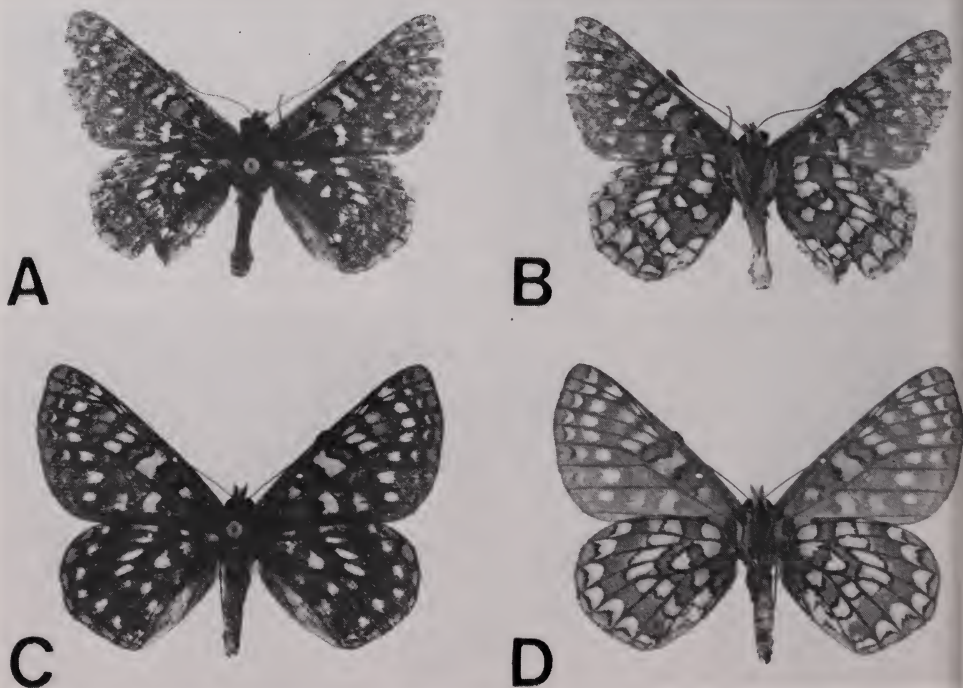
Fig. 7.   Equivocal *Euphydryas* pair from Deer Creek, Boise Nat. For., Valley Co., Idaho, 24.vii.84. A. Male, dorsal. B. Male, ventral. C. Female, dorsal. D. Female, ventral. All C. D. Ferris Coll.

is an extreme variant of the *anicia* phenotype. Occasional dark indi-
viduals occur in many *anicia* populations, perhaps as a consequence of
thermal shock during the prepupal stage.

Various authors have suggested that *paradoxa* McDunnough (usually
referred to *chalcedona*) represents a stable hybrid between *chalcedona*
and *anicia*. It is not the intent of this paper, however, to review species
that occur outside of Idaho.

Conclusion

On the basis of my studies in Idaho and the data presented above, I
conclude that the taxa *anicia* and *chalcedona* represent closely related
but separate species. They can be distinguished by differences in the
male genitalia and FW maculation. Their flight periods overlap, with
chalcedona on the wing from mid-May into late July depending upon
geographic location and elevation. *E. anicia* generally appears in early
July and survives into August at suitable elevation.

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The Mating System of *Vanessa kershawi:* Males Defend Landmark Territories as Mate Encounter Sites

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Abstract. Males of *Vanessa kershawi* (McCoy) occupy perch territories in the late afternoon in sunspots on hilltops and other locations in southwestern Australia. Perching males respond to intruders with chases and ascending flights, with some individuals defending the same perch site for several consecutive afternoons. Females visit territories strictly to mate and not to use any resources in these areas. In the absence of hilltops males wait at sites where local topography and vegetation create passageways that might channel dispersing females to them. Landmark-based mating systems of this sort appear to evolve in species whose females are highly dispersed because of the distribution of the food and oviposition resources that they exploit.

Introduction

Although the painted lady butterflies — genus *Vanessa* — are common and widespread, relatively little is known of their reproductive behavior. Accounts of *V. atalanta*, *V. cardui*, *V. caryae*, and *V. indica* indicate that males of these species go to certain conspicuous landmarks, particularly hilltops, but also forest-meadow edges, where they perch in the late afternoon (Alcock, 1984; Bitzer & Shaw, 1979(80); Niimura, in Suzuki, 1976; Scott, 1975, 1986; Shepard, 1966; Shields, 1967). Although males of some species are territorial, defense of the perch site does not occur in several of these species when population densities are high (Alcock, 1984). It has been assumed that perched males on hilltops and other landmarks are awaiting the arrival of receptive females, but no observations of copulations at these sites have been recorded in the literature.

This report describes the reproductive behavior of *V. kershawi* (Mc-Coy), an abundant species throughout Australia (Common & Waterhouse, 1972). Some authors consider *V. kershawi* to be a subspecies only of *V. cardui* (Zimmerman, 1958), and there is no question that the two are very similar. We show that this butterfly uses landmarks as mate-encounter sites but that in different locations males establish territories at very different kinds of landmarks. We discuss the significance of this finding for an understanding of landmark-based mating systems, as well as documenting that landmark territoriality is associated with mate-acquisition in this species.

Methods

The butterflies were observed on 6−7 October at Tutanning Reserve, approximately 25 km east of Pingelly and 175 km southeast of Perth, W. A., on 18−19, 23−24 October and 19−20 November at Watheroo National Park, W. A., in the south-central portion of the park about 250 km north of Perth, and from 29 October to 13 January at King's Park, an area of natural bushland in Perth, W. A. The descriptive data were largely collected by selecting a site that contained a male perched on the ground in the late afternoon and then recording the behavior of the male or males that resided in that location for periods ranging from 10 min to 2.5 hr. In some cases resident males were captured in an insect net and marked with Liquid Paper typewriter correction fluid through the folds of the net before being released. The sites at which males were observed were checked again on subsequent days to determine if some perch sites were used repeatedly.

Means are presented ± 1 S.D.

Results

Perch Site Selection

In all three study sites, males arrived at their perching sites on the ground in sun spots or sunny strips in the mid- to late-afternoon. Although on some days males arrived as early as 1500 hr, the density of perching males was greatest between 1700−1800 hr in all three places. All males were gone from their perching areas by dusk. But the vegetation and topography of the areas in which males chose perch sites varied considerably among the three locations. At Tutanning, males selected sun spots on moderately forested hilltops, particularly on the edge of rocky escarpments, but also on the flat "plateaus" of the hilltops, sometimes dozens of meters from the steep hillsides. The sunspots were scattered among a forest of *Eucalyptus wandoo* and *Casaurina huegliana*.

In King's Park there are no well-defined hilltops but instead gently rolling terrain with gradual ascents and descents. At this site males were found throughout the area perched on concrete pathways (Fig. 1) and cleared firebreaks, with no obvious concentrations on the higher elevations. The paths and firebreaks cut through a forest of *Banksia*, *Casaurina* and *Eucalyptus marginata* in places and elsewhere through more open stretches of tall shrubs, mainly blackboys (*Xanthorrhea preissii*).

In Watheroo National Park the terrain was almost completely flat and the forest an open one composed of pricklybark (*Eucalyptus todtiana*), scattered *Banksias*, and zamia palms (*Macrozamia reidlei*). Males perched in sunny avenues in the woodland, particularly in one area where low pricklybark foliage formed a green barrier; the descending sun illuminated a long strip of ground parallel to the barrier.

Territorial Behavior

Perching males flew up at objects moving near them including stones and chunks of wood thrown over them, as well as flying dragonflies, other butterfly species, and even birds. In addition perched males sometimes spontaneously flew 2−10 m away from their perch before returning to land usually at or near the previous perching area. These spontaneous "patrol flights" occurred at the rate of 8.7/hr based on 360 min of observation of focal males in the three locations.

If at any time, a conspecific male entered the perching area, a chase invariably resulted. Whereas chases of non-conspecifics lasted only a few seconds, chases of fellow males regularly lasted about 30 sec ($\bar{X} =$ 28.9 ± 17.0 sec, N = 36, range 7−75). Chases began with horizontal dashes, roughly 5−15 m in length and oriented back and forth over the territory. Chases lasting more than 10−15 sec usually terminated with rapid ascending flights that took the participants 5 or more meters high, far away from the territory and out of view of the observer in woodland habitats.

The frequency of male-male interactions varied from 18.4/hr (based on 5 hr of observation) at Tutanning to 5.7/hr (11.3 hr of observation) at King's Park, and 4.7/hr (4.25 hr of observation) at Watheroo. Generally only one male returned from a chase to perch at the site which had been occupied before the interaction. Thus males used chases to monopolize perching sites and to disperse their rivals. At King's Park and at Watheroo perching males were separated by at least 25 m on most days. At the highest density site (Tutanning Reserve) a maximum of 11 males occupied an area of 1452 m² with a minimum distance of 6.3 m between nearest neighbors ($\bar{X} = 9.1$ m, N = 9). Note that it was at this site that interactions among males were most frequent.

Some males were able to control a territory for substantial periods of time in an afternoon. At King's Park we secured 15 records of identified males (either marked with Liquid Paper or with distinctive wing damage) that held their site for a minimum of 30 min in an afternoon (up to a maximum of 140 min). Six marked males showed considerable site tenacity by returning to their perch site on the same day as capture, despite the trauma of netting. Residents generally succeeded in repelling intruders, winning 46 of 53 interactions sampled on seven days and involving five different residents at King's Park. On four occasions both resident and intruder returned to perch in the same general area and only in three cases did the intruder replace the resident.

Some males were also able to reclaim the same location on several days. In the 10 day period from 9−18 November, all resident males (10) at one territory in King's Park were identified by marks or wing damage, and the area checked daily. Table 1 shows that during this time three territory owners returned to the site on more than one day. In addition, a different male defended the same location for the four days
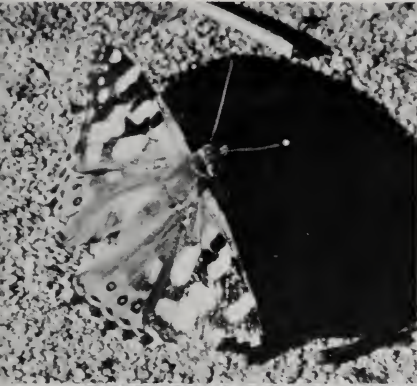
Fig. 1. A male *Vanessa kershawi* perched in a sunspot on a concrete sidewalk slab in King's Park, Perth.

Fig. 2. A frequently occupied perching area in King's Park, Perth. Males defended concrete slabs in the left hand lane of the track in the middle of the figure. Note that the surrounding vegetation creates a tunnel of sorts over the perching area.

Fig. 3. A copulating pair of *Vanessa kershawi* that mated after the female flew to the male's landmark territory on a hilltop in Tutanning Reserve, W.A.

between 26−29 November. Thus at least under some conditions males exhibit site tenacity.

But the competition for perch ownership also led to turnovers. On seven occasions when observing an identified male at King's Park or Tutanning, a new male replaced the past owner after a chase or series of chases. Thus some perches attracted more than one male owner in a single day (see Table 1), and the same spot could be occupied over a series of days by many different males. At Watheroo one site that was held on 19, 23−24 October was also claimed a month later on 19 November. A focal territory at King's Park was held by six different residents during 9−18 November and at least four other males visited the site. The recorded number of visitors is surely a gross underestimate of the actual total because most intruders were promptly chased away before they could be captured, marked or identified. The focal territory at King's Park was occupied by a resident male on 20 of 22 afternoons when the site was checked from 29 October to 13 January. Three other sites on a transect of King's park paths 420 m long were also occupied on a majority of these days (Site B = 15/22, Site C = 13/22, and Site D = 14/22).

Male-Female Interactions

Encounters between males and females were rare. At Tutanning Reserve two matings were recorded, both at times of peak male density:

Table 1. Resident and visitor males of *V. kershawi* at one perching site in King's Park, Perth from 9−18 November 1985. R = resident male — present for most of observation period; v = visitor male — present only for brief period(s) before being chased away by the resident male; R* = new male takes site from previous resident site during an afternoon.

November Male		9	10	11	12	13	14	15	16	17[1]	18
	A	R	R	R							
	B	v									
	C			v		v	R				
	D			v							
	E			v	R	R		R			
	F					R*					
	G							R*			
	H								R		
	I								R*		
	J										R

[1]no observations made on this day

1729 hr on 6 October and at 1733 hr on 7 October. These took place at two different territories on the edge of a hilltop when a female flew into a territory, and was pursued by the resident away from the perch site. The pair flew much more slowly and more erratically than male-male interactors, and with no ascending component to the chase. In both cases the two butterflies landed on the foliage of a sapling wandoo eucalyptus, approximately 24 and 5 m from the point of first encounter, respectively. The male landed by the female, facing in the same direction. Copulation followed quickly with no preceding wing-fluttering by the female in one instance, although in the other the female flew off the perch several times before alighting for good. Once the female had ceased moving, the male simply probed with his abdomen twisting it to the side to couple with the female, after which he turned to face directly away from his partner (Fig. 2). In both cases copulation was still in progress 1 hr after its initiation.

One mating was recorded at King's Park at 1707 on 16 November. It followed the same pattern, although in this case the female led the male on a long pursuit as she flew away from and then returned to pass over the perch territory several times before finally landing on a casaurina cone some 3 m above the ground and about 10 m from the perch site. Copulation was still in progress 30 min after it began.

Two other probable male-female interactions were seen at King's Park. One occurred at 1648 on 11 November when a male visitor with a distinctive wing mark that had been perching near the territory holder suddenly flew up after another visitor and departed. The pair flew off in the distinctive, relatively slow horizontal flight that characterized male-female pursuits but the butterflies were lost to view in the woodland. The male did not return within a hour. The second inter-action took place at 1715 on 18 November when an individual, probably a female, flew into a male's territory and led him on a brief chase before landing on the ground. The male perched immediately behind the visitor and flew up when it left. The pair went into the woodland in a slow horizontal pursuit flight and were lost in the scrub. The male did not return within a minute as was normally the case in male-male chases.

Discussion

The term "territoriality" covers a variety of behavioral phenomena, but in its most widely accepted sense it refers simply to the defense of space by an individual (Brown, 1975). In this sense males of *V. kershawi* are territorial, with individuals defending perches that may be visited in the late afternoon by receptive females. The distinctive features of male-male chases, which are very different from male-female encoun-ters and pursuits of heterospecifics, leave little doubt that male-male interactions determine ownership of a perch site. Similar behavior has been labelled "territorial" in two reviews of insect territoriality (Baker,

1983; Fitzpatrick & Wellington, 1983; but see Scott, 1986, for arguments on the absence of territoriality in butterflies).

Some perch sites are consistently occupied by many different males over a period of several months; other similar locations never attract a territory owner. What properties make a perching area worth defending? There are no flowering plants or oviposition resources in the territories of *V. kershawi*; females visit perched males solely to acquire a mate and males defend their perching areas solely to maintain a site from which to scan for incoming females. We suggest that the mating system of *V. kershawi* is based on landmarks with local topography dictating where females are most likely to be travelling, and this in turn determines where males compete for waiting sites.

As is true for a host of butterflies and other insects, prominent hilltops may serve as orientation guides or attraction points for females (Scott, 1970; Shields 1967; Thornhill & Alcock, 1983), and when hilltops are available (as at Tutanning Reserve) males of *V. kershawi* wait at the highest points. But in some regions, hilltops are absent and then males use alternative topographic features as productive waiting sites. In King's Park, many territories are on walking tracks, sidewalks and firebreaks at points where the trailside vegetation creates a passageway likely to channel or funnel passing females toward a perched male. Similarly at Watheroo males appear to wait in open sunny areas in the woodland through which traveling females might be guided by the foliage of plants beside the clearings. Thus, whatever their environment, males of *V. kershawi* seem to take advantage of natural orientation marks, clearings through vegetation, and foliage barriers to station themselves at points most likely to be visited by dispersing females. Males of other Lepidoptera that use landmarks as mate-encounter sites may also be using topographic channels and funnels that concentrate travelling females (Callaghan, 1982(83)).

Flexibility in the use of landmarks also occurs in other butterflies (Scott, 1982(83)), including *V. atalanta* (Alcock, 1984; Bitzer & Shaw, 1979(80)), whose males station themselves on peaktops in hilly or mountainous terrain, but wait in clearings and forest-meadow edges in flat, forested areas.

The use of landmark and topographic guides appears widespread in the genus *Vanessa* (Alcock, 1984; Bitzer & Shaw, 1979(80); Shields, 1967). The behavior of *V. kershawi* and *V. atalanta*, for example, is close to identical in terms of sites selected by waiting males, the nature of male-male interactions, the duration and frequency of aerial chases, the consistency with which some territories are defended from day to day, and the restriction of territoriality and mating to the late afternoon (Bitzer & Shaw, 1979(80); Dimock, 1984(85)). Why should males of these butterflies be so prone to wait at resource-less areas rather than searching actively for females at foraging or oviposition sites? The general rule among insects is that when either food or egg-laying

resources are concentrated, thereby concentrating females spatially, males focus their search at these locations (Thornhill & Alcock, 1983). In many butterflies, including *Vanessa* species whose larvae and adults feed on a wide range of hosts (Common & Waterhouse, 1972), females are often not clumped and therefore are not easy to locate (Rutowski, 1984). Under these circumstances males may be forced to wait in portions of their environment where travelling females may occasionally appear (Rutowski, 1984). *Vanessa* butterflies are well-known for their tendency to travel long distances (Johnson, 1969; Smithers, 1969).

One would predict, however, that if females of a *Vanessa* species happened to become aggregated at a restricted food- or hostplant, their males would respond by searching for mates at these productive locations. When females of *V. cardui* occur in large numbers on flowering *Encelia farinosa* in central Arizona, some males do search for mates at the foodplant (Alcock, 1984). A combination of hilltopping and searching at flowers has been reported for a few other butterflies as well as by Scott (1982(83), 1986). Likewise, 10–20 males and females of *V. kershawi* were found at a local patch of a flowering *Verticordia* on 19–20 November at Watheroo National Park. The plant had not been in bloom a month earlier when late afternoon perch defenders were common in other areas, but by 19–20 November only a single perch defender was located. Instead, throughout these days males frequently engaged in what appeared to be brief (< 5 sec) horizontal sexual chases at the foraging site. Apparently when females of *Vanessa* are spatially clustered at flowers, males travel to these locations to search for receptive partners. But if no such clusters exist, males wait at travel points for diffusely distributed females to come to them.

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Apodemia palmerii (Lycaenidae: Riodininae): Misapplication of Names, Two New Subspecies and a New Allied Species

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Abstract. The subspecific names of *Apodemia palmerii*, *A. p. palmerii* and *A. p. marginalis*, have been variously used for the phenotypes of the species. Examination of the types and series of topotypes indicates that they are synonymous. New subspecific names are proposed for the darker phenotype distributed east of the Colorado River drainage and another in central Mexico. Southern Baja California, Mexico populations, often referred to as *Apodemia "palmerii"* are described here as a new species.

Introduction

William Henry Edwards (1870) described *Lemonias palmerii* from Utah. Subsequently, Skinner (1920) named the taxon *Lemonias palmerii marginalis* from a California population of the species. The name *"marginalis"* has been variously treated as a form synonymous with Edwards' concept (dos Passos 1964, Howe 1975, Miller and Brown 1981, Austin 1985b) or as a recognizable subspecies distinct from nominate *A. palmerii* (Comstock 1927, Holland 1931, Emmel and Emmel 1973, Tilden 1975, Austin and Austin 1980). Populations from southern Arizona and western New Mexico generally have been referred to as nominate *A. palmerii* (Comstock 1927, Holland 1974, Howe 1975, Ferris 1976). Study of material from throughout the range of the species and examination of the type specimens of the two presumptive subspecies indicate errors in the application of *A. p. marginalis* and that new names are needed for the *A. palmerii* populations east of the Colorado River drainage and those in Mexico. Yet another phenotype, previously referred to as *A. palmerii* (Rindge 1948, Holland 1972), occurs in southern Baja California, Mexico, but it is, in fact, an undescribed species.

Throughout this paper, butterfly size (given as mean and range) is the length of the right primary from the base to the apex in millimeters. Measurements are for 15 specimens unless otherwise indicated. Specimens indicated by "M" and "F" are male and female, respectively.

Names and Populations

The description of the male of *Apodemia palmerii* was based on Utah material taken by Edward Palmer (Edwards 1870). Later, Edwards (1884b) stated that his description was based on a single male. Brown (1967, 1968) presented ample evidence that the specimen was most likely collected in Utah, probably in the vicinity of St. George, Washington County during June 1870. The holotype male (Brown 1968) at the Carnegie Museum of Natural History is a typical spring brood specimen with entirely orange margins. Skinner's (1920) description of *A. p. marginalis* was based on two males and a female from Acme (once called Morrison, *ca.* 4 miles south of Tecopa), Inyo County, California. He distinguished it from supposed nominate *A. palmerii* by its orange wing margins (hence the name *"marginalis"*) and by its pallidity. No mention was made of either the geographical or seasonal source(s) of the material to which he compared his types. A male [holo]type and a female [allo]type are among the type material transferred to the Carnegie Museum of Natural History from the Academy of Natural Sciences of Philadelphia (see also Gillham and Ehrlich 1954). These were collected by Morgan Hebard on 8 August 1919 and represent the typical pale late summer phenotype.

I first became aware of a possible nomenclatural problem during my studies of southern Nevada butterflies (Austin and Austin 1980). My series from this area was of a seasonally variable, dark to pallid, orange-margined butterfly which was obviously distinct from the darker southern Arizona insect. It seemed unlikely on biogeographic and ecological bases that nearly all Colorado River basin populations were of one phenotype while southern Utah examples should be a disjunct population of the same sort as found in southern Arizona. I, therefore, collected representative series from eastern California near the type locality of *A. p. marginalis*, from southern Utah in the St. George region (the designated type locality of *A. palmerii*) and from southern Arizona (Pima, Cochise and Pinal counties). I also took a small number from western Arizona (Maricopa and Mohave counties). These along with material borrowed from various museums and collectors indicate that two phenotypes are indeed involved in this region but that the names available have been inappropriately applied.

The distribution of the species *Apodemia palmerii* includes extreme northeastern Baja California, Mexico; the southeastern, desert portions of California; southern Nevada; extreme southwestern Utah; south and eastward through southern Arizona and southwestern New Mexico to western Texas (Fig. 1). It occurs in northwestern and northcentral Mexico (where its distribution is incompletely known, Hoffmann 1976), but it occurs south into the central portions of the country (to Hidalgo and Michoacan) and in the western states of Sonora and Sinaloa. The southern Baja California populations also traditionally have been treated as this species.
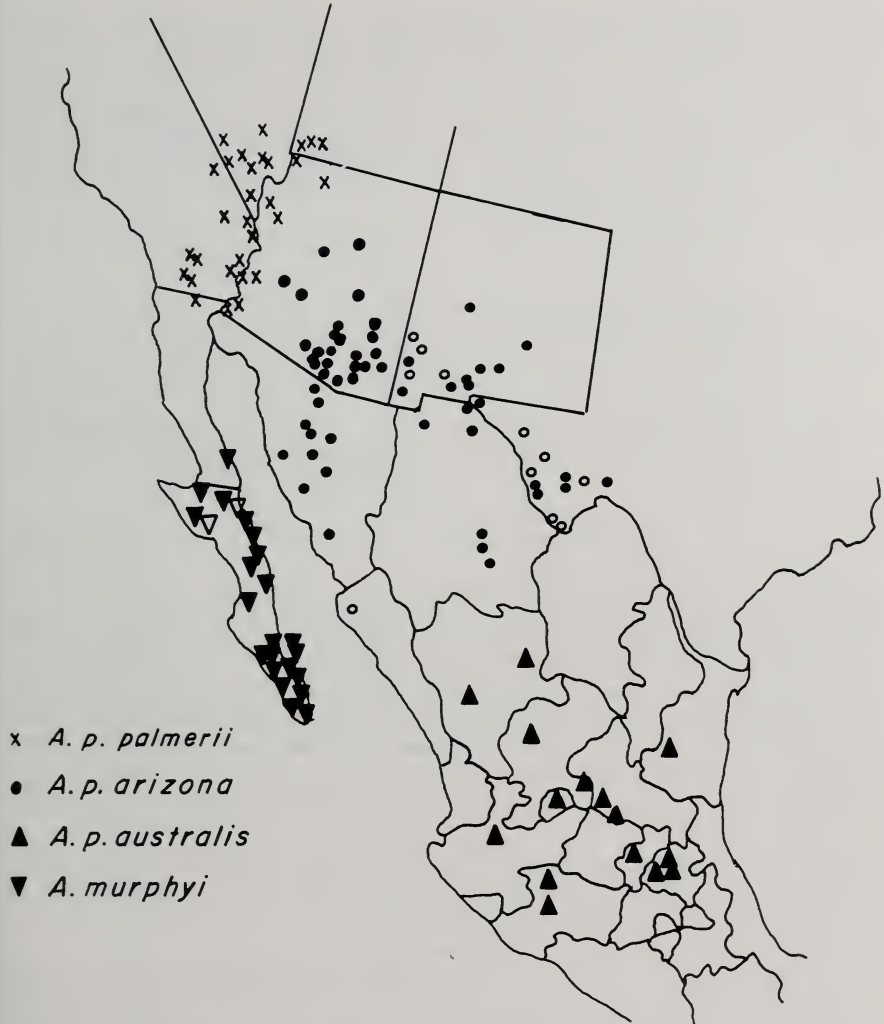
x *A. p. palmerii*

• *A. p. arizona*

▲ *A. p. australis*

▼ *A. murphyi*

Fig. 1. Distribution of *Apodemia palmerii* sspp. and *Apodemia murphyi* (open symbols indicate specimens not examined).

A pale phenotype with prominant orange margins from the Colorado River drainage and nearby areas of California, Nevada, Utah and western Arizona generally has been referred to as *Apodemia palmerii marginalis*. The darker populations from east of the Colorado River drainage, on the other hand, have been considered nominate *A. palmerii*. No other names have been applied to other variations within the species. While Edwards' description must serve as that for the species, it is not detailed enough to distinguish that phenotype from others in question. Skinner's description unquestionably refers to the pale pheno-type. The application of the name *"marginalis"* was, in my opinion,

probably based on comparisons with Arizona material since Arizona specimens are more widely represented in collections than those from southern Utah. My experience is that *A. palmerii* is uncommon in the St. George region, even where good stands of its foodplants, honey mesquite (*Prosopis glandulosa* Torr.) and screwbean mesquite (*P. pubescens* Benth.) are available. The species, however, is abundant in similar situations in southern Arizona.

Apodemia palmerii palmerii (W. H. Edwards, 1870) (Fig. 2)

Lemonias palmerii W. H. Edwards (1870, p. 195), Kirby (1871, p. 650), W. H. Edwards (1872, p. 38), W. H. Edwards (1874, p. 38), W. H. Edwards (1877, p. 38), Kirby (1877, p. 760), Strecker (1878, p. 104), Brooklyn Entomological Society (1881, p. 3), W. H. Edwards (1884a, p. 294), W. H. Edwards (1884b, p. 301), Maynard (1891, p. 126), Skinner (1898, p. 43), Smith (1903, p. 6), Snow (1907, p. 156)

Chrysobia palmerii Scudder (1876, p. 103)

Lemonias palmeri Holland (1898, p. 231), Skinner (1904, p. 16), Wright (1905, p. 202), Haskin (1914, p. 306)

Polystigma palmerii Dyar (1902, p. 34)

Apodemia palmerii Mengel (1905, p. 120), Stichel (1911, p. 288), Seitz (1924, p. 700), Barnes and Benjamin (1926, p. 16), Stichel (1930, p. 590), McDunnough (1938, p. 23), dos Passos (1964, p. 51), Brown (1967, p. 129), Scott (1979, p. 191), Fisher *in* Ferris and Brown (1981, p. 198–199), Miller and Brown (1981, p. 132), Pyle (1981, p. 530), Miller and Brown *in* Hodges (1983, p. 57)

Apodemia palmerii palmerii Stichel (1911, p. 288), Brown (1968, p. 121), Callaghan and Tidwell (1971, p. 198), Austin (1985a, p. 128), Austin (1985b, p. 107).

Apodemia palmeri Barnes and McDunnough (1917, p. 13), Holland (1931, p. 213), Ehrlich and Ehrlich (1961, p. 245), Tietz (1972, p. 504), Powell *in* Howe (1975, p. 270), Gillette (1983, p. 15).

Lemonias palmerii marginalis Skinner (1920, p. 175)

Apodemia palmerii from "marginalis" Barnes and Benjamin (1926, p. 16), McDunnough (1938, p. 23), Martin and Truxal (1955, p. 20), dos Passos (1964, p. 51), Hoffmann (1976, p. 68), Fisher *in* Ferris and Brown (1981, p. 198–199), Miller and Brown (1981, p. 132), Miller and Brown *in* Hodges (1983, p. 57)

Apodemia palmerii marginalis Comstock (1927, p. 151), Comstock and Dammers (1932, p. 37), Davenport and Dethier (1937, p. 170), Emmel and Emmel (1973, p. 49), Tilden (1975, p. 30)

Apodemia marginalis Holland (1931, p. 213)

Apodemia palmeri marginalis Gillham and Ehrlich (1954, p. 102), Emmel (1972, p. 3), Austin and Austin (1980, p. 23)

Apodemia palmeri form "marginalis" Tietz (1972, p. 504), Powell *in* Howe (1975, p. 270)

Apodemia palmeri palmeri Austin and Austin (1980, p. 23)

Specimens of *Apodemia palmerii* from southwestern Utah, southern Nevada, southeastern California, extreme western Arizona and extreme northern Baja California Norte, Mexico (essentially the Colorado River and Death Valley

2a   2b

Fig. 2a. *Apodemia palmerii* subspecies (dorsal surface). Top left — *A. p. arizona*
holotype male, AZ: Cochise Co.; Az. 90, 14.6 mi. N Az. 82, 4 Sept. 1980,
leg. G. T. Austin. Top right — *A. p. arizona* allotype female, same data.
Second left — *A. p. palmerii* topotype male of form "marginalis", CA: Inyo
Co.; 0.3 mi. N Tecopa, 8 Sept. 1981, *leg*. G. T. Austin. Second right — *A. p.
palmerii* topotype female of form "marginalis", same data. Third left — *A.
p. palmerii* male of form "marginalis", NV: Clark Co.; Whitney Mesa at
Sunset Rd., 6 Sept. 1977, *leg*. G. T. Austin, Third right — *A. p. palmerii*
female of form "marginalis", NV: Clark Co.,; Las Vegas, Paradise Valley,
6 Sept. 1977, *leg*. G. T. Austin. Fourth left — *A. p. palmerii* male, NV: Clark
Co.; Las Vegas, Paradise Valley, 24 May 1978, *leg*. G. T. Austin. Fourth
right — *A. p. palmerii* female, same data. Bottom left — *A. p. australis*
holotype male, MEXICO, Durango 1 mi. S. Nombre de Dios, 1760 m, 30
Aug. 1973, *leg*. L. D. and J. Y. Miller, Bottom right — *A. p. australis*
allotype female, same data.

Fig. 2b. *Apodemia palmerii* subspecies (ventral surface). Same specimens as in
Fig. 2a.

drainage basins, Fig. 1) are virtually identical in their general pallidity, in the
presence of continuous orange margins on the dorsal surface of both wings, and
in seasonal variability (Fig. 2). This geographical extent encompasses the type
localities of both *A. p. palmerii* and *A. p. marginalis*. The latter name thus is
clearly synonymous with the nominate and refers to the pale late summer/
autumn form. Examination of the types confirmed this. The butterfly is often
locally abundant and flies in three to four broods in southern Nevada (Austin
and Austin 1980) and two to three broods in southern California (Emmel and
Emmel 1973).

Nominate *Apodemia palmerii* is seasonally variable. Early season (April-
June) specimens are generally large (male $\bar{x}$ = 11.2, range = 10.6−11.8,; female
$\bar{x}$ = 12.5, range = 11.7−13.1, May sample) and relatively dark with a restriction
of the fulvous on the wing bases, especially on males. Later (July-October)
specimens are smaller (male $\bar{x}$ = 10.1, range 9.0−10.9; female $\bar{x}$ = 11.2, range

10.2−12.2, September sample) and paler with considerable fulvous on the wings. The type specimen of *A. palmerii* was illustrated by Brown (1968). Holland (1931) figured a paratype of form "marginalis" but his indicated "type" of *A. palmerii* is a pseudotype (Brown 1968, see below). Emmel and Emmel (1973) illustrated a male of the spring phenotype. Holland (1931), Emmel and Emmel (1973) and Howe (1975) illustrated form "marginalis". Comstock and Dammers (1932) described and illustrated the life history of a California population. The larval host plants are *Prosopis glandulosa (= P.juliflora)* and *P. pubescens* (Fabaceae) (Comstock and Dammers 1932, Austin and Austin 1980).

This then leaves populations exhibiting somewhat darker phenotypes from outside this area without names. To rectify this situation, I describe here two new subspecies.

Apodemia palmerii arizona new subspecies **Austin** (Fig. 2)

Lemonias palmerii Kirby (1871, p. 650), Kirby (1877, p. 760), W. H. Edwards (1877, p. 38), W. H. Edwards (1883, p. 9), W. H. Edwards (1884a, p. 294), W. H. Edwards (1884b, p. 301), Maynard (1891, p. 126), Skinner (1898, p. 43), Smith (1903, p. 6), Snow (1904, p. 337), Snow (1907, p. 156)

Chrysobia palmerii Scudder (1876, p. 103)

Apodemia palmeri Edwards (1882, p. 28), Godman and Salvin (1886, p. 468), Barnes and McDunnough (1917, p. 13), Holland (1931, p. 213), Rindge (1948, p. 300), Ehrlich and Ehrlich (1961, p. 245), Powell *in* Howe (1975, p. 270), Austin (1978, p. 210)

Lemonias palmeri Godman and Salvin (1886, p. 468), Holland 1898, p. 231), Skinner (1904, p. 16), Haskin (1914, p. 306), Stone (1921, p. 114).

Polystigma palmerii Dyar (1902, p. 34)

Apodemia palmerii Mengel (1905, p. 120), Stichel (1911, p. 288), Seitz (1924, p. 700), Barnes and Benjamin (1926, p. 16), Stichel (1930, p. 590), McDunnough (1938, p. 23), Bauer (1954, p. 100), Martin and Truxal (1955, p. 20), dos Passos (1964, p. 51), Brown (1965, p. 112), Lewis (1973, p. 112), Tilden (1974, p. 24), Hoffmann (1976, p. 68), Fisher *in* Ferris and Brown (1981, p. 198−199), Miller and Brown (1981, p. 132), Pyle (1981, p. 530), Miller and Brown *in* Hodges (1983, p. 57), Austin (1985b, p. 107)

Apodemia palmerii palmerii Comstock (1927, p. 151), Brown (1968, p. 123), Holland (1974, p. 44), Ferris (1976, p. 46)

Apodemia palmeri palmeri Austin and Austin (1980, p. 23)

MALE. Dorsal ground color dark brown, sometimes nearly blackish-brown. Basal one-third of both wings usually fulvous, often with considerable black overscaling. White markings and their associated black outlines much as on *Apodemia palmerii palmerii*. Marginal area usually of ground color, especially apically, with small areas of fulvous in each cell (not broadly fulvous), these fulvous areas usually broader posteriorly on both wings and usually somewhat overscaled with ground color. Ventral ground color largely fulvous with markings of dorsum repeated but larger. Distinct submarginal black points on both wings.

Male genitalia virtually identical to those of *Apodemia palmerii palmerii*.

FEMALE. Somewhat larger in size than male with a more rounded (less pointed) apex to primaries. Color and pattern similar to male.

TYPES (data as on labels, clarified in brackets). Holotype male — A[RI]Z [ONA]: Cochise Co. [unty]; A[ri]z[ona State Route] 90, 10.8 mi. [les] N. [orth of]

A[ri]z[ona State Route] 82, 7 Sept.[ember] 1980, *leg*. G. T. Austin. Allotype female — same data as holotype. Paratypes (32M, 26F) — same data as holotype (26M, 21F); some data as holotype except 14.6 mi. N (6M, 4F); same data as holotype except 8.4 mi. N (1F).

DEPOSITION OF TYPE MATERIAL. The holotype, allotype, 11M and 6F paratypes will be deposited in the type collection of the Nevada State Museum. A pair of paratypes will be deposited in each of the following institutions: Allyn Museum of Entomology, American Museum of Natural History, National Museum of Natural History, Carnegie Museum of Natural History, Natural History Museum, San Diego, and Los Angeles County Museum. The remainder are to be retained by the author.

TYPE LOCALITY. ARIZONA: Cochise County, Arizona State Route 90, 10.8 miles north of Arizona State Route 82. The types were collected on the west side and within 100 feet of the road. Most were perched on mesquites (*Prosopis glandulosa*) (Fabaceae) which undoubtedly serves as the larval host plant.

DISTRIBUTION AND PHENOLOGY. *Apodemia palmerii arizona* occurs from Arizona south and eastward through southwestern New Mexico to western Texas, south into at least Chihuahua, Sonora and Sinaloa, Mexico (Fig. 1). The subspecies has at least two (but probably more) broods in southern Arizona (Austin 1978) and two broods in southwestern New Mexico (Ferris 1976). In southern Arizona, Brown (1965) reported it as a late rainy season species although Austin (1978) found it to occasionally have a large spring brood, at least in years with spring rainfall.

ETYMOLOGY. This subspecies is named for its type locality, the state of Arizona.

DIAGNOSIS AND DISCUSSION. The new taxon, *Apodemia palmerii arizona*, is at once distinguished from nominate *A. palmerii* by the largely dark margins of the dorsum of both the primaries and secondaries. This same area of *A. palmerii* is broadly fulvous with considerably less or no ground coloration. A very few *A. p. arizona* approach *A. p. palmerii* in this respect just as occasional *A. p. palmerii* have the margins somewhat darkened. The dorsal ground color of *A. p. arizona* is darker and with less fulvous flush basally than *A. p. palmerii* giving the impression of an overall darker butterfly. Some late season females of *A. p. palmerii* are very pale with the ground color approaching a pale tan (a condition I have not seen among *A. p. arizona*). The ventral color is paler than the average early season *A. p. palmerii* but somewhat darker than late season material. The submarginal black points are larger and more distinctly indicated than on nominate *A. palmerii*. An aberrant female from Patagonia, Arizona (5 Sept. 1951) has the postmedian and basal white markings absent on all wings; the submarginal markings are normal.

There is no appreciable seasonal variation in *Apodemia palmerii arizona* and late season specimens have the size (male $\bar{x}$ = 11.5, range = 10.6−12.0; female $\bar{x}$ = 12.4, range = 11.6−13.2, September sample) and a comparable dark ground color of early season *A. p. palmerii*. The figures in Howe (1975) adequately illustrate *A. p. arizona*. Edwards (1884b) and Holland (1931, as the type of *A. p. palmerii*) also illustrate this taxon. Edwards (1884b) described and illustrated the egg and young larva from southern Arizona.

Apodemia palmerii arizona, at least, applies to southern Arizona, southern New Mexico and adjacent northwestern Mexico populations (Fig. 1). The few specimens I have seen from the extreme eastern portion of its distribution in

Texas (but not near El Paso) and east central Chinhuahua (but not north-western) consistently have broader white markings and are somewhat larger (female x̄ = 13.2, range = 12.4−14.3, N = 7) but otherwise closely fit the concept.

Material from central Mexico is yet darker dorsally and browner ventrally. It is recognized as follows:

Apodemia palmerii australis new subspecies **Austin** (Fig. 2)

Apodemia palmeri Godman and Salvin (1887, p. 709), Holland (1931, p. 213), Ehrlich and Ehrlich (1961, p. 245), Powell *in* Howe (1975, p. 270)

Lemonias palmeri Holland (1898, p. 231)

Lemonias palmerii Skinner (1898, p. 43)

Apodemia palmerii Seitz (1924, p. 700), Fisher *in* Ferris and Brown (1981, p. 198−199), Pyle (1981, p. 530)

MALE. Dorsal ground color blackish with slight fulvous basal overscaling on secondaries and occasionally on primaries, white markings as on other *Apodemia palmerii* subspecies but often smaller in size. Outer margins with fulvous indistinct, usually restricted to small area at anal angle of primaries and posterior half of secondaries. Ventrum dull brownish-orange ground color, apex of primaries and entire secondaries dark tan, markings of dorsum repeated, black submarginal points minute.

Genitalia of typical *Apodemia palmerii* type with broadly rounded uncus, hooked upper process of valve, distinctly rounded vinculum and relatively short saccus.

FEMALE. Wings more rounded than male, color and pattern similar on both surfaces, ventral black submarginal points larger.

TYPES. (data as on labels, clarified in brackets). Holotype male — MEXICO: Durango; 1 mi[le] S[outh] Nombre de Dios, 1760 m[eters elevation], desert scrub, 30 viii [August] 1973, *leg*. L. D. & J. Y. Miller, Sta. No. 1973−53. Allotype female — same data as holotype. Paratypes (all MEXICO: Durango; 43M, 20F) — same data as holotype (37M, 7F, AME); 1.5 mi. SW Durango, 1920 m, ground scrub, 28 Aug. 1973, (5M, 5F, AME); Durango, 6200′, 13 Aug. 1947 (1M, 5F, AMNH); Durango, 1 Aug. 1964 (1F, CIS); Yerbanis, Cuencame Dist., 19 Aug. 1947 (1F, AMNH); Nombre de Dios, 5900′, 13 Aug. 1947 (1F, AMNH).

DEPOSITION OF TYPE MATERIAL. The holotype, allotype, 41M and 11F paratypes are deposited at the Allyn Museum of Entomology; 1M and 7F paratypes are at the American Museum of Natural History; 1F paratype is at the California Insect Survey; and one pair of paratypes are retained by the author.

TYPE LOCALITY. MEXICO: Durango; 1 mile south of Nombre de Dios, 1760 meters. The vegetation here is desert scrub with trees to 25 feet in height, some mesquites (*Prosopis*), various other low trees with a grass undergrowth on a valley floor (*fide* L. D. Miller).

DISTRIBUTION AND PHENOLOGY. This subspecies occurs mostly in the central mountains of Mexico from Durango to Hidalgo and Michoacan usually above 4500′ in elevation (Fig. 1). There are at least two broods with records in April (once), May (once) and from mid July through mid September, most records are for August.

ETYMOLOGY. This phenotype is the most southerly distributed of the species, thus the name *"australis"* (= southern).

DIAGNOSIS AND DISCUSSION. This is a very dark *Apodemia palmerii* subspecies, appearing nearly black when fresh. Individuals are considerably darker above than those from other known populations of the species and lack a conspicuous basal flush of fulvous. The white spots average small and sometimes appear smudged. Ventrally this butterfly is brown rather than distinctly fulvous as are both of the more northern subspecies. The basic pattern, wing shape and the structure of the male genitalia leave no doubt that this subspecies falls within the range of variation expected of *A. palmerii*. It approximates the size of other *A. palmerii* (male x̄ = 11.5, range = 10.6–12.5; female x̄ = 12.6, range = 11.3–13.2).

An even more distinctive series of populations occurs in the southern portions of Baja California, Mexico. This heretofore has been called *Apodemia palmerii* but closer examination reveals that this is a very different insect with a unique combination of characters. This new species is here described as:

Apodemia murphyi new species **Austin** (Fig. 3)

Apodemia palmeri Rindge (1948, p. 300), Powell *in* Howe (1975, p. 270)
Apodemia palmerii Holland (1972, p. 156), Fisher *in* Ferris and Brown (1981, p. 198–199), Pyle (1981, p. 530)

MALE. Dorsum with blackish-brown ground color. Late summer and fall (July-mid November) specimens usually with well-defined fulvous basal area; winter and spring (late November–April) specimens heavily overscaled with ground color on this area, often black without fulvous. White markings as on *Apodemia palmerii palmerii* and *A. p. arizona* but considerably reduced in size, especially on primaries. Marginal area mostly of ground color except for, usually, posterior one or two cells on each wing, these with small areas of fulvous.

Ventral ground color brownish-orange, markings of primaries repeat dorsal pattern but tending slightly larger. Ventral secondaries with white markings considerably larger than dorsally, those in postmedian area form a continuous broad band. Wings narrow, apex of primaries very long and pointed, often approaching subfalcate.

Genitalia similar to *Apodemia palmerii* but with several subtle differences as discussed below.

FEMALE. Similar to male except dorsal white markings larger and more fulvous marginally, especially posteriorly on secondaries. Shape of primaries more rounded than on males but with distinctive tendency towards a subfalcate tip. Seasonal variation similar to male.

TYPES. Holotype male — MEXICO: Baja California Sur; Arroyo San Bartolo, 28 Aug. 1982, *leg*. [J. W.] Brown and [D. K.] Faulkner (SDNHM). Allotype female — same data as holotype (SDNHM). Paratypes (all MEXICO: Baja California Sur; 103M, 54F) — same data as holotype (2M, 1F, SDNHM); A. San Bartolo, 3 Nov. 1961 (2M, CM), 12 Nov. 1961 (2M, 1F, CM); San Bartolo, 3 Oct. 1981 (2M, 1F, SDNHM); 2 mi. S of Buena Vista, 30 Nov. 1979 (3M, 1F, SDNHM); Buena Vista at Monument Rd., 4 Jan. 1980 (1F, JB); 3 mi. S Rio Buenavista, 25 Oct. 1961 (2M, CM); 5 km S Rio Buenavista, 25 Oct., 1961 (2M, CM); 4.2 mi. W. Miraflores, 30 Sept. 1981 (1M, SDNHM); Miraflores, 25 Oct. 1961 (1M, CM), beach, Todos Santos, 26 July 1981 (6M, SDNHM); estuary at Todos Santos, 26 July 1981 (9M, 2F, CM), 31 July 1981 (2M, CM), 20 March 1974 (4M, 1F, CM); E1 Pescadero, 20 March 1974 (1F, CM); 1/4 mi W Todos Santos, 20 March 1974 (2M, SDNHM), 19–20 March 1974 (3M, GF); 14 mi N Todos Santos, 4 Oct. 1981 (1M, 1F, SDNHM); Santiago, 6 Nov. 1946 (1M, 3F, SDNHM); 19 mi. SE El Cien,

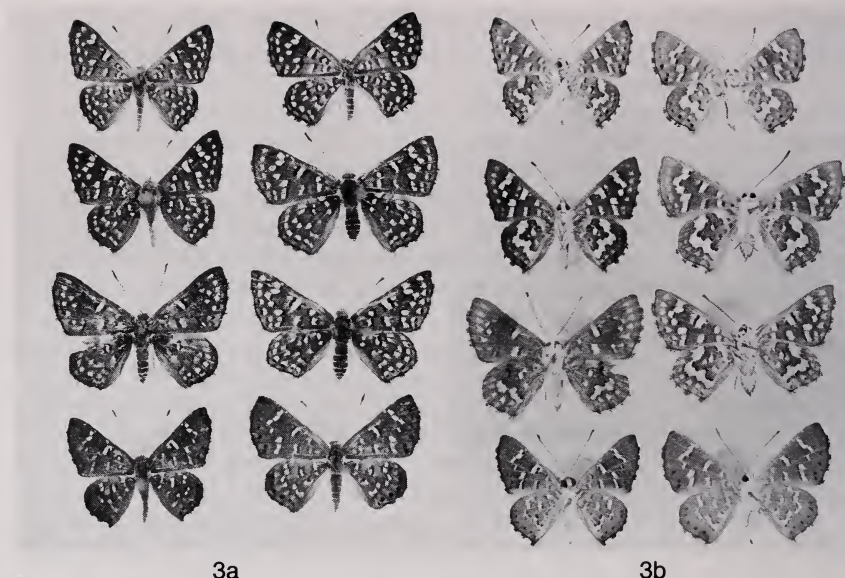3a   3b

Fig. 3a. *Apodemia murphyi* and *Apodemia hepburni* (dorsal surface). Upper left
— *A. murphyi* holotype male, MEXICO: Baja California Sur; Arroyo San
Bartolo, 28 Aug. 1982, *leg*. Brown and Faulkner. Upper right — *A. murphyi*
allotype female, same data. Second left — *A. murphyi* male dark
phenotype, MEXICO: Baja California Sur; 12.2 mi. SE San Perdito near
Rancho Saucito, 8 Oct. 1981, *leg*. F. Andrews and D. Faulkner. Second
right — *A. murphyi* female dark phenotype, MEXICO: Baja California Sur;
7 mi. SE Guerrero Negro, 8 Apr. 1976, *leg*. Doyen and Rude. Third left —
A. murphyi aberrant female, MEXICO: Baja California Sur, 10 mi. N Bahia
Asuncion, 25−27 April 1984, *leg*. Bloomfield. Third right — *A. murphyi*
normal female, same data. Bottom left — *A. hepburni* male, MEXICO:
Baja California Sur; 2 mi. SW Cadauno, 26 Aug. 1982, *leg*. Faulkner and
Brown. Bottom right — *A. hepburni* female, same data.

Fig. 3b. *Apodemia murphyi* and *Apodemia hepburni* (ventral surface). Same
specimens as in Fig. 4a.

27 Sept. 1981 (1M, 1F, SDNHM); Cabo Pulmo, 4 Nov. 1946 (1M, SDNHM);
1.5 mi. SW San Jose del Cabo, 30 Sept. 1981 (3M, SDNHM); San Jose del Cabo,
17 Feb. 1940 (4M, SDNHM), 1 July 1968 (1M, CM), 22 Nov. 1961 (1F, CM); 3 mi.
N San Jose del Cabo, 22−23 Nov. 1961 (2M, 5F, CM); Cabo San Lucas, Hotel
Finisterra, 8−10 Oct. 1979 (1M, 1F, SDNHM); Cabo San Lucas, 22 March 1939
(1F, AMNH), no date (1M, AMNH), 2 Apr. 1949 (1M, SDNHM), 23 Nov. 1961
(1M, CM); 20 mi. N Cabo San Lucas, 29 Sept. 1970 (1F, CM); 15 mi. S La Paz, 1
Nov. 1946 (5M, 2F, SDNHM); La Paz airport, 10 Oct. 1979 (1F, SDNHM); 7 mi.
SW La Paz, 4 Aug. 1966 (1F, SDNHM); La Paz, 17−22 Sept. 1967 (1M,
SDNHM), 9 July 1968 (2F, CM); 13 Sept. 1959 (1M, CM); La Paz, Guaycura
Hotel grounds, 6−8 Nov. 1961 (5M, 1F, CM); SE shore La Paz Harbor, 5 Nov.
1961 (1M, CM), 10 Nov. 1961 (5M, CM); E shore, La Paz Bay, 8 Nov. 1961 (6M,
8F, CM); 3 mi. S Santiago, 25 Oct., 1961 (1F, CM); Las Barracas, *ca*. 30 km
E Santiago, 7/12 Apr. 1982 (1M, CIS); Puerto Chileno, 22 Nov. 1961 (1M, CM);
Boca de la Sierra, 17−24 Nov. 1961 (1M, 2F, CM); Ro. Palmarito, 27 Oct.−5 Nov.

1961 (2M, 2F, CM); Rancho El Salto, 28 Oct. 1961 (1M, CM); Bahia de Palmes, 20 Nov. 1961 (2F, CM); Isla Espiritu Santo, 19–23 Feb. 1936 (1F, SDNHM), 17 April 1958 (1M, LACM), 14 July 1985 (1M, SDNHM), 30 Dec., 1938 (3M, 3F, AMNH); San Jose I., Gulf of California, 5 March 1975 (1F, UCD); Isla Partida, 17 April 1958 (1M, LACM); Bahia Agua Verde, 20 April 1958 (2M, LACM); 31 km N Todos Santos, 29 Nov. 1980 (1F, SDNHM); 7 km S Candauno [sic], 26 Aug. 1982 (2F, SDNHM); Punta Conejo, *ca.* 32 km SW El Cien, 9 Jan. 1977 (1M, G. T. Austin); Todos Santos Rd., *ca.* 42 km N Cabo San Lucas, 14 Jan. 1977 (1M, G. T. Austin); Muertos Bay, 24 March 1939 (1M, AMNH), 29 Dec., 1938 (1M, AMNH).

DEPOSITION OF TYPE MATERIAL. The holotype, allotype, 36M and 17F paratypes are deposited at the Natural History Museum, San Diego; 51M and 31F paratypes are in the Carnegie Museum of Natural History; 6M and 4F paratypes are in the American Museum of Natural History; 4M paratypes are in the Los Angeles County Museum; 1M paratype is in the collection of the California Insect Survey; 1F paratype is at the Bohart Museum, University of California, Davis; 1F paratype is in the private collection of J. Brock; 3M paratypes are in the private collection of G. S. Forbes; and 2M paratypes are in the author's private collection.

TYPE LOCALITY. MEXICO: Baja California Sur; Arroyo San Bartolo. San Bartolo is on Mexico Highway 1 between La Paz and San Jose del Cabo. All specimens examined from south of 25°N latitude are designated paratypes.

DISTRIBUTION AND PHENOLOGY. *Apodemia murphyi* occurs throughout much of Baja California Sur and to extreme southern Baja California Norte, Mexico (Fig. 1). Its northern limit appears to be the Bahia de las Animas and Bahia de Los Angeles area on the east coast (Rindge 1948, Holland 1972). No records of an *Apodemia palmerii*-like butterfly exist north of this point (Rindge 1948, Powell 1958, Patterson and Powell 1959, Holland 1972) for nearly 450 km virtually to the United States border (one specimen of *A. p. palmerii* from Mexicali, Baja California Norte, AME) although Hoffmann (1976) indicated that *A. p.* "marginalis" is found in Baja California.

The insect is apparently continuously brooded and has been collected in every month. The majority of specimens (127 of 250 examined with dates) are from October, November and December. This may reflect collecting patterns rather than phenological patterns of the butterfly. Fresh specimens occur throughout the year.

ETYMOLOGY. I name this insect after Dennis D. Murphy to whom I owe numerous debts.

DIAGNOSIS AND DISCUSSION. The taxon *Apodemia murphyi* is most distinctive. It is about the size of *Apodemia palmerii* but the sexes are nearly the same (male x̄ = 11.7, range = 10.4–13.2; female x̄ = 11.6, range = 10.8–12.7, October sample). The basic pattern above is similar to *A. palmerii arizona* but the white spots are smaller in size (but are distinct and not smudged as on some specimens of *A. p. australis*). The ventral pattern is very different from any *A. palmerii*, especially the secondaries with the broad (up to *ca.* 25% of wing surface) and continuous white postmedian band. On *A. palmerii* this band is disjunct and more of a sinuous series of spots. The shape of the primaries is different from any *A. palmerii* being more drawn out and pointed towards the apex, especially on the male, and subfalcate. The fulvous basal area of the wings is sharply set off from the dark distal area, particularly on summer and fall specimens. These areas grade into one another on *A. palmerii*.

An interesting aberrant female was seen (MEXICO: Baja California Sur; 10 mi. N Bahia Asuncion, 25–27 April 1984, *leg.* Bloomfield, SDNHM; Fig. 3). Most of the postmedian white spots of the dorsum are absent. Those present along with the basal white spots are small. These are similar on the ventral primaries and the typical postmedian of the secondaries is absent anteriorly and narrowed posteriorly. The black submarginal macules and the black lines associated with the postmedian are nearly obsolete. This is not as extreme as the aberrant *A. p. arizona* noted above. Aberrations are rare among the Riodininae with none described for the North American fauna (Kendall and McGuire 1984).

The male genitalia, while similar to those of *Apodemia palmerii*, differ in several respects (note above that genitalia of *A. palmerii* are constant over the entire range of the species). Overall, the structures are slightly more massive although the aedeagus is proportionally shorter, terminating just beyond the lower arm of the valve (extends considerably further posteriorly on *A. palmerii*). The uncus is relatively narrow (dorsal aspect) and rounded (posterior aspect). The uncus of *A. palmerii* is broader with more rounded lobes and flatter. The falces are stouter on *A. murphyi*, the dorsal arm averages slightly longer and the ventral arm is considerably shorter than on *A. palmerii* (dorsal arm: ventral arm = 0.7 for *A. murphyi*, 0.5 for *A. palmerii*). The valves of *A. murphyi* are broader and stouter with a pointed (but not hooked) upper process. The saccus is proportionally longer on *A. murphyi* and the vinculum is straighter and not broadly rounded ventrally as on *A. palmerii*.

Apodemia murphyi resembles *Apodemia hepburni* Godman and Salvin in wing shape and the continuous postmedian band on the ventral secondaries (Fig. 3). The latter is otherwise distinctive with a less complete spot pattern (lacking the submarginal series among others), no clear basal fulvous area on the dorsal primaries and a considerably narrower postmedian band on the ventral secondaries. The figures show these characters clearly. *Apodemia hepburni* is sympatric and synchronic with *A. murphyi* at many localities from Mulege southward. *Apodemia hepburni* records extend from 26 August through 6 April; *A. murphyi* from 26 July through 8 April at these localities. Label data (also *fide* J. W. Brown) indicates that *A. murphyi* nectars commonly on *Bebbia juncae* (Asteraceae) and also on *Melochia tomentosa* (Sterculiaceae) and *Baccharis* sp. (Asteraceae). The species is associated with *Prosopis glandulosa* (Fabaceae) throughout its range; this probably is a larval host plant.

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SPECIMENS EXAMINED

Apodemia palmerii palmerii

UNITED STATES: Arizona (37M, 23F; 27 March-7 September): Coconino, Mohave, Yuma counties; CALIFORNIA (321M, 206F; 15 March-12 November): Imperial, Inyo, Riverside, San Bernardino, San Diego counties; NEVADA (211M, 126F; 17 April-13 October): Clark, Lincoln, Nye counties; UTAH (43M, 29F; 20 May-13 September): Washington County. **MEXICO:** BAJA CALIFORNIA NORTE (1F; August).

Apodemia palmerii arizona

UNITED STATES: ARIZONA (type series plus 407M, 335F; 17 April-24 October): Cochise, Coconino, Gila, Graham, Maricopa, Pima, Pinal, Santa Cruz, Yavapai counties; NEW MEXICO (19M, 15F; 12 May-11 September): Dona Ana, Hidalgo, Lincoln, Luna, Otero, Socorro counties; TEXAS (8M, 25F; 13 April-9 September): Brewster, El Paso, Presidio, Terrell counties. **MEXICO**: CHIHUAHUA (2M, 6F; 14 July-31 August); SINALOA (1M, 1F; 28 June); SONORA (35M, 31F; 12 March, 3 August-25 October).

Apodemia palmerii australis

MEXICO: AGUASCALIENTES (1M; 27 August); DURANGO (type series plus 16M, 1F; 30 July-20 August); HIDALGO (4M, 9F; 30 April, May, 19 July-8 August); JALISCO (1M, 26 July); MICHOACAN (15M, 3F; 9 August); QUERETARO (2F; 20 July); SAN LUIS POTOSI (5M, 5F; 20 July-23 August); TAMAULIPAS (4M; 20 September); ZACATAS (1M, 1F; 30 August).

Apodemia murphyi

MEXICO: BAJA CALIFORNIA NORTE (1M, 3F; 30 March, 19 September-6 October); BAJA CALIFORNIA SUR (type series plus 80M, 33F; 7 March-28 June, 11 August-December including 5M at AME and 1M, 1F at SDNHM labeled Baja California Norte).

OTHER RECORDS

Apodemia palmerii

UNITED STATES: NEW MEXICO; Catron, Grant counties (Ferris 1976); TEXAS: (31 March-7 October; Tilden 1974, Freeman 1981): Culberson, Jeff Davis, Pecos counties (Tilden 1974, *fide* R. O. Kendall).

Apodemia murphyi

MEXICO: BAJA CALIFORNIA NORTE (8 May; Rindge 1948).

Correlations of Ultrastructure and Pigmentation Suggest How Genes Control Development of Wing Scales of *Heliconius* Butterflies

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Introduction

In the last two decades there have been extensive genetic studies of the mimetic wing patterns of *Heliconius* butterflies (Turner, 1981; Sheppard *et al.*, 1985), but these analyses have not probed the precise nature of color patterns at the ultrastructural level. Thus, while many ecological and evolutionary phenomena have been elucidated, the nature of the genes involved and the mode of their action in the course of wing pattern development remains obscure.

One another front there is renewed interest in general models of pattern formation in butterfly wings (Nijhout, 1986), but studies of pattern development have relied upon comparisons among related species or upon experimental manipulations of wing development within species. Remarkably, there has been a lack of genetical analysis applied to the problem of butterfly wing pattern development on the one hand, and little attention given to the chemical and ultrastructural basis of "color pattern" on the other, although excellent studies have been carried out on chemistry (e.g., Umebachi and Yoshida, 1970; Descimon, 1975) and ultrastructure (e.g., Ghiradella, 1974; 1985) separately.

In an attempt to refine genetic hypotheses which explain the variation of wing pattern observed in crosses involving different races and species of *Heliconius* (Sheppard *et al.* 1985; Gilbert, in prep.), it appeared

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appropriate to investigate the chemical and morphological basis for color and pattern. This paper summarizes our initial investigations of wing scale structure and chemistry on four species of *Heliconius* which have been subjects of genetic studies in the senior author's laboratory.

The findings presented for *Heliconius* below provide the first clear evidence from lepidopteran wings that genetic control of pigmentation patterns simultaneously involves patterns of differentiation in scale ultrastructure, a result anticipated in general terms by Descimon (1965). Thus, beyond elucidating the connections between genes and wing patterns in butterflies, the results suggest that *Heliconius* wings may provide a useful system for addressing general questions about the genetics of pattern development.

Material Examined

All butterflies for ultrastructural and chemical studies were reared in greenhouses at Patterson Laboratory, The University of Texas at Austin. *Heliconius* species examined included *Heliconius cydno galanthus* (stock origin, La Selva, Costa Rica), *Heliconius pachinus* (stock origin, Osa Peninsula, Costa Rica), *Heliconius melpomene rosina* (stock origin, Osa Peninsula, Costa Rica), and *Heliconius ismenius clarescens* (stock origin, Osa Peninsula, Costa Rica). Hybrid "bar-shadow" regions (explained below) were from F1 hybrids of the *H. cydno* and *H. pachinus* stocks above. In addition, forewing red/brown scales were examined in *H. cydno — H. melpomene* crosses. Illustrations of these species may be found in DeVries (1987) and of their hybrids in Gilbert (1984).

Because a wide variety of methods are used in this study, necessary details of techniques will be provided below.

SCALE MORPHOLOGY

Scales were examined by standard methods of scanning electron microscopy. Dry wing fragments with uniform scale color were coated with 25Å of gold-palladium in a Hummer V sputter coater and examined at 600 and 10,000X using an ISI Super IIIA. Scale cross sections were created by cutting wing fragment with a razor blade and searching that area for appropriately cut scales.

Descriptive terminology used below follows the system developed by Downey and Allyn (1975). It should also be stressed that while we are confident in distinguishing the following major scale types, interpretation of many morphological details is tentative.

Type I scales. Yellow/white (Fig. 1 A, B, C, D; Fig. 5B; Fig. 6A)

In *Heliconius*, yellow and white scales appear to represent the same morphological type. Average spacing of scute peaks (=lamellae of Ghiradella, 1985) along the ridge is approximately the same as the inter-ridge distance. Obverse membrane obscures the scale internal

structure. Many variable sized windows may occur in the membrane, especially in the central region of the scale. Transverse flutes (=micro-ribs of Ghiradella, 1985) run over the membrane surface between, and perpendicular to, longitudinal ridges. Such flutes are evenly spaced and occur at a density of 8-10 per inter-scute interval.

White and yellow scales appear to lack crossribs, and scale cross sections show trabeculae primarily below longitudinal ridges.

The spacing of ridges in Type I scales is narrower on the dorsal wing surface, so that dorsal wing scales often have 1.5 to 2 times the number of ridges per scale width as do ventral wing scales (compare Fig. 1B vs. 1A). This ultrastructural difference may help account for the sheen and richer colors of the dorsal versus the ventral wing surfaces.

Type II scales. Black (Fig. 2A, B, C, D; Fig. 5A, C; Fig. 6B)

The melanic scales of *Heliconius* possess longitudinal ridges con-nected by ladder-like crossribs, most of which are supported by trabe-culae. Crossribs appear more narrow than ridges and are arranged in poorly aligned rows. There is usually no obverse membrane in melanic scales and flutes are visible only on the vertical walls of longitudinal ridges.

As in Type I scales, ridges are spaced more widely on ventral wing scales than on dorsal scales. In both *H. cydno galanthus* and *H. pachinus*, dorsal scales noted as "dull" proved to have more widely spaced ridges than those noted to be "shiny" (e.g., Fig. 2C vs. 2B).

Type II′ Hybrid "bar-shadow" scales. Black (Fig. 3A, B, C)

The "bar shadow" is a region of altered reflectance on the melanic region of a hybrid *Heliconius* ventral hindwing. This region corresponds to the location of yellow scales in one parent race of a cross, the other parent of which possess a totally melanic hindwing. The bar shadow is used to diagnose hybrid genotypes in ecological genetic studies (Mallet, 1986).

These scales are identical to Type II scales except that roughly 5% of spaces between crossribs are covered by obverse membrane (Fig. 3). In some cases the membrane is intact over the inter-rib space, but in most cases these scales resemble partly dissolved tissue draped over chicken wire. This subtle change is visible to the naked eye, but not under light microscope. This scale type might be viewed as a small step toward a morphological hybrid of Type I and Type II scales. However the membrane, where present, lacks supportive flutes and the scales are otherwise identical to Type II scales.

Type III scales. Reds and browns (Fig. 4A, B, C, D; Fig. 5D; Fig. 6C)

"Red and brown" scales in *Heliconius* include orange, orange-brown, brown, pink, and red scales. These share a basic morphology, Type III. Crossribs often appear to be wider than those of Type II scales, and one

or two strengthening flutes pass over each crossrib, connecting adjacent ridges. In addition, obverse membrane appears to be retained over each crossrib and immediately adjacent to longitudinal ridge. This may account for the thicker appearance of ridges and ribs in Type III scales, as well as the angular appearance of crossribs.

Cross sections of Type III scales do not reveal trabeculae supporting presumptive crossribs, but they can be seen supporting longitudinal ridges, and may simply occur less frequently than in Type II scales. Without further detailed work, it is not possible to exclude the possibility that strips of membrane supported by flutes function as pseudo-crossribs rather than overlay them as suggested above. Close examination of Type III scales suggests their closer relationship to Type I than to Type II scales. For example, the inter-ridge space on the left extreme of the brown scale in Fig. 4A is virtually identical to the obverse membrane of a dorsal Type I scale (e.g., Fig. 1B). These characteristics gradually change to typical Type III features toward the center of the scale. Like Types I and II, Type III scales typically possess more narrow spacing of the longitudinal ridges on the dorsal wing surface.

Scale Chemistry

White Scales: No pigment

White scales of *Heliconius cydno* possess a highly reflective quality or sheen quite unlike the flat white of *Pieris*. Under light microscope at low power, these scales are brighter where two or more overlap. These observations suggested a structural rather than chemical basis for the white color.

To test this possibility, scales were immersed in a solution whose refractive index is near that of chitin (1.55). When single scales were observed in such a solution (xylene or Permount) against a black background, they became essentially transparent. Scales in xylene regain their white luster when the liquid evaporates. Comparisons with yellow and black scales indicate that luster, but not color, disappears in these liquids. Uric acid tests were negative on chromatographs of Type I scale areas. White scales in *Heliconius* are therefore due to structural features of the scale rather than pigments.

Yellow Scales: 3-hydroxykynurenine

A small circle of the yellow part of the wing was cut out with a cork borer, and positioned carefully at the aperture of the Cary Recording Spectrophotometer. Measurement of the UV spectrum revealed peaks at 282nm and 405nm (a rather broad peak). These are essentially identical to the peaks produced by 3-hydroxykynurenine in 0.1N NaOH (pH 14) (285 and 395nm).

Extraction of the pigment using water or dimethyl sulfoxide and

rerunning the spectrum of this extract in 0.1N NaOH or 0.1N HCl gave
the following values:

λ *max 0.1N NaOH*	λ *max 0.1N HCl*
280(285)	252(252)
395(395)	312 shoulder(312)

3-hydroxykynurenine peaks (in parentheses)

These data indicate that the yellow pigment in *Heliconius* spp. is the
alkaline form of 3-hydroxykynurenine. This pigment is previously
described from *Heliconius* (Brown, 1967).

An interesting question concerns the maintenance of 3-hydroxyky-
nurenine in its alkaline form in the wing scales of *Heliconius*. Chro-
matographic studies were carried out to elucidate this phenomenon.
Fragments of yellow wing areas of *H. pachinus* were ultrasonicated,
then agitated in 80% methanol. This extract was spotted on Whatman
No. 1 filter paper and subjected to one dimensional chromatography
using BAW, n-butanol/acetic acid/water (4:1:1) as solvent. A ninhydrin
test (1g of ninhydrin dissolved in 50ml acetone; chromatograph was
immersed in this solution, allowed to dry, and heated at 110°F until color
developed) revealed that an amino acid or peptide was located in the
identical spot with the alkaline form of 3-hydroxykynurenine (revealed
by UV light).

A comparison with white scales using the same procedure showed the
identical ninhydrin sensitive spot, but no yellow pigment. Two-dimen-
sional chromatographic studies of all basic amino acids using the same
solvent, BAW, did not duplicate the spot derived from *Heliconius* wing
extract. It is therefore likely that a peptide or small polypeptide is
responsible for keeping 3-hydroxykynurenine in the alkaline state. The
precise location of this complex within the scale is not yet determined.

Black Scales: melanin

Chromatographic evidence verified that black scales contain melanin
but tryptophan is also present in extracts of black scales. Melanic scales
embedded in paraffin, sectioned, and examined with light microscope
revealed that pigment is found in the walls of ridges and in crossribs.

Brown and Red Scales: xanthommatins

Wings were extracted with dimethyl sulfoxide (DMSO) or with 2%
HCl in methanol. The spectrum of the extracts and of standard com-
pounds are given in Table 1. There are two problems of interpretation
with these data. First, the spectra of xanthommatin and dihydroxan-
thommatin are notoriously difficult to reproduce because of rapid
decomposition and slight changes in state of reduction (see Linzen,
1974). Second, it was not possible to make comparisons of extracted

Table 1.   Extraction methods and absorbance values (nm) of chemical standards and wing pigments of *Heliconius* (*Values from Denys, 1982)

PIGMENTS	EXTRACTION	ABSORBANCE MAXIMA (nm) CONDITIONS						
		DMSO	pH7-7.5	Acid Methanol	5N HCl	2% Digitoxin pH6.5	2% Digitoxin pH10.4	
Brown from H. ismenius	DMSO	440-450,365						1
	DMSO acidified to 5N HCl				450,360			2
	acid methanol			450, no distinct peak at 360				3
Red from H. melpomene	DMSO	490,365						4
	DMSO extract + acetone/ether; resulting ppte. in H2O pH7.0		465,368					5
	acid methanol			448, no distinct peak at 360				6
Red from H. pachinus	acid methanol			458,360-380				7
	acid methanol, oxidised with NaNO2			448				8
Brown from pure sample xanthommatin	dissolved as indicated		440		475-480, 370-375	*450	*478	9
Red from pure sample dihydro-xanthommatin	dissolved as indicated		505-510	475-360	500(shoulder), 390			10
	Reduced with NaBH4			490,370				11
		1	2	3	4	5	6	

pigments from *Heliconius* wings with standard samples of xanthommatins under absolutely identical or controlled conditions. However, taken as a whole, the data indicate first that the major brown or red pigments of *Heliconius* butterflies are xanthommatin and dihydroxanthommatin and second, that variations in color from bright red to brown are due to variations in the state of oxidation of dihydroxanthommatin (or the state of reduction of xanthommatin).

First note the correspondence in the spectral maximum between the brown pigment of *H. ismenius* and that of xanthommatin (Table 1, row 1 and 2 versus row 9). Further note the DMSO extract of *H. melpomene* red pigment (Table 1, row 5, col. 1), the spectrum of which peaks near that of dihydroxanthommatin under reduced conditions (Table 1, row 11, col. 3). Obviously these extracts of red dihydroxanthommatin are in various stages of oxidation to xanthommatin.

Given the in vitro instability of the reduced red form of xanthommatins, the observed stability of various shades of orange and red on the wings of various races of *H. melpomene* and *H. erato* presents an

interesting mystery. However, the likelihood that 3-hydroxykynurenine is maintained in an alkaline state by a gene product suggests that such associations may allow races to "select" localized pH conditions within Type III scales by modification of a peptide or protein associated with xanthommatin pigment, and thereby affect subtle variation in the actual color displayed on the wing.

Evidence from *H. cydon X H. melpomene* crosses indicates genetic control of separate factors maintaining the reduced form of xanthommatin (red) in *H. melpomene*. Thus, in all F1 hybrids of *H. pachinus* or *H. cydno* with red forewing banded *H. melpomene* races (illustrated in Gilbert, 1984), brown scales appear on the ventral side of the dorsal forewing red band, and with appropriate crosses, one can convert the dorsal red forewing band of hybrids to brown (Gilbert, unpublished data).

Discussion

Different hypotheses can be proposed for how genes determine final color patterns in *Heliconius*. At one extreme, scale morphology and pigmentation would be separately determined by independently regulated genes such that any combination of structure and color could occur. This possibility is not the case in *Heliconius* because of melanic scales (including bar-shadow scales), which are consistently found to have a particular subset of ultrastructures, scales with Type I ultrastructure which consistently lack melanin or xanthommatin, and Type III scales are never white, yellow, or melanic.

At the other extreme, genes which determine pigment production in a developing scale might pleiotropically determine its ultrastructure. This would be the case if the product of a single gene directly or indirectly regulates both morphological events and the pigment pathway within a scale. In *Heliconius*, this possibility appears to hold true at the level of major pigmentation differences (eg. xanthommatin vs. melanin). However, some pigment variation such as brown vs. red in Type III scales, or white vs. yellow in Type I scales, represents minor pigment variation within the major categories. We hypothesize that such minor variation in Type III scales is based on variation in genes coding for those peptides which act to stabilize pigments at particular oxidation states in the scales.

Any useful model for scale development in *Heliconius* should explain the observed correlations of structure and pigmentation (summarized in Table 2) in genetic and chemical terms. It should also be in general accord with current knowledge of scale development, pigment chemistry, and genetics. Fortunately, development of scale pigmentation has been carefully studied in another nymphalid genus, the pigments involved are relatively well-studied in other systems, and extensive classical genetics is available for *Heliconius*.

With respect to scale development, Nijhout's (1980) observations and experiments provide a useful model for the development of different colored melanic scales in *Precis* (Nijhout, 1980, p.287).

1. Enzymes for pigment synthesis are insoluble but active within cuticle of the scale.

2. Substrates for pigment synthesis circulate in the hemolymph and are produced in sequence.

3. Substrates can gain access to scales at all times.

4. Scales in each presumptive color region possess only a single enzyme and are capable of utilizing only a single substrate.

Nijhout (1980) also observed that longitudinal ridges formed before melanin deposition, indicating that the pigment per se only stiffens the scale, but does not direct its morphogenesis. We therefore assume that in *Heliconius*, any pleiotrophic effects of genes involved in pigment pathways on scale structural distinctiveness is not via the pigment, its precursors, or substrates. Rather it seems most likely that the product of a "scale selector" gene acts as a turn-on switch for other genes involved in scale ultrastructure on the one hand, and genes for pigment pathway enzymes on the other.

Our interpretations of the chemistry of yellow, red, and brown variation in *Heliconius* benefit from the extensive genetic and biochemical work on *Drosophila* eye color variation which is based on the same ommochrome pathway (Summers *et al.*, 1982). Xanthommatin pigments derive from tryptophan via intermediates such as kynurenine (Linzen, 1974), but two lines of evidence suggest that the substrate for xanthommatin production is 3-hydroxykynurenine. First, in *Drosophila* eyes, normal xanthommatin production depends on external kynurenine and/or 3-hydroxykynurenine supplied via the hemolymph (Summers et al., 1982). Second, Linzen (1970) reviews evidence that a) in holometabolous insects, including Lepidoptera, tryptophan accumulation in hemolymph and other tissues is transitory and b) 3-hydroxykynurenine is the metabolite most likely to persist at elevated levels. Thus, it is reasonable to assume that the substrate for xanthommatin in *Heliconius* Type III scales is 3-hydroxykynurenine.

Similarly, although melanins arise ultimately from oxidation of tyrosine, the substrates for melanin production are likely to be dopa or dopamine if *Heliconius* follows the usual pattern for insects (Wigglesworth, 1972) and for *Precis* wing scales (Nijhout, 1980).

Association of xanthommatin and other ommochromes with specific proteins in silkworm blood (see Linzen, 1974 for review) make our suggestions about mechanisms of color fine-adjustment and stability a credible working hypothesis. On the other hand, reports of ommochromebinding protein in cecropia moth eyes (Ajami and Riddiford, 1971) have not been verified in parallel studies on *Drosophila* (Wiley and Forrest, 1979), nor have the subtle variations in *Drosophila* eye color been adequately explained.

Additional parts of the *Heliconius* scale puzzle are provided by genetic evidence. Certain genes for xanthommatin scales (Type III) are dominant (Sheppard *et al.*, 1985) or epistatic (in single dose) to those for melanic scales (Type II) (Gilbert, in prep.) in *H. melpomene*. Other dominant or epistatic genes, active in the same regions of the wing, may replace yellow scales (Type I) with melanic or xanthommatin containing scales (see Sheppard *et al.*, 1985). We suggest these observations are due to our hypothesized scale selector genes, the interaction of which generally produces an unambiguous scale type in the following order of dominance or epistasis: III > II > I. Bar shadow scales on the ventral hindwing may represent an exception to this rule if they indeed possess intermediate features.

Genetic variation for pigmentation within scale types appears to have no common theme. In Type I scales, white is dominant to yellow (see F1 of *H. cydno* X *H. pachinus*, (Gilbert, 1984). This is counter to what we would expect if the heterozygote simply possesses one half the amount of yellow pigment. We hypothesize a gene involved with transport of 3-hydroxykynurenine into the developing Type I scale. The bar shadow variant of Type II scales (II') probably reflects dosage of Type II selector gene, M, (but only expresses on one wing surface!). Color variation of xanthommatin pigments may be due to a structural gene for the binding peptide as previously discussed.

At this stage of knowledge, many alternative models of *Heliconius* scale development might be equally difficult to reject. With this caveat, we present a model which is consistent with the observed relationships of scale structure and color (Table 2) and which assumes as valid, the foregoing points about scale development, pigment chemistry, and genetics. Finally, for simplicity, we develop the model as a series of binary choices which depend upon the state of scale selector genes in cells which give rise to the scales. The following model should be considered a tentative scheme rather than a well-substantiated theory.

During the course of development, cells would be fated to give rise to a particular scale type at a particular wing location by the combination of selector genes which are switched on or off. The threshold conditions for such switching might allow trichogen cells of the same genotype to end up as different scales types depending upon the strength of morphogen signals at that location (see Nijhout, 1986).

A fundamental decision in scale development seems to be between Type I versus Type II or III, because Type I scales do not require pigment to stiffen, and are apparently not manufacturing complex pigments from simple substrates. For simplicity, we consider this scale type the null state, that scale type which develops if no other selector genes are switched on.

Next, if Type II selector switch gene M is turned on, cells are fated to develop Type II or Type III scales. Given that only M is on, and given appropriate positional information, the M + signal would turn on

Table 2. A summary of the relationship between scale morphological types and scale pigmentation observed in the four *Heliconius* species and two interspecific crosses of this study. Type II′ refers to the bar shadow scale type, yellow, brown, and red refer to 3-hydroxykynurenine, xanthommatin, and dihydroxanthommatin respectively (see text).

PIGMENTATION

SCALE TYPE	none	yellow	brown	red	melanic
I	X	X			
II					X
II′					X
III			X	X	

morphological programs and melanin pathway enzymes. However, the scale would not melanize and stiffen until dopa or dopamine circulate in the hemolymph.

In keeping with a binary decision model of genetic determination, we suggest that the selector gene for Type III scales, X, can only be expressed in M + cells, and that its signal initiates Type III morphology and turns on genes for xanthommatin pathway enzymes. Genetic evidence summarized above indicated that M++X+ cells give rise to Type III, xanthommatin containing scales.

Thus, it appears that the xanthommatin pathway inhibits in melanin pathway by a method similar to its inhibition by another oxidative pathway, xanthopterine synthesis (Wigglesworth, 1972). Since in *Heliconius* pupae, homozygous and heterozygous forewing Type III patches develop xanthommatin well ahead of the melanization of Type II areas (Gilbert, unpublished observation), it may be that the pigment itself inhibits the oxidation of substrates of the melanin pathway as is the case with xanthopterine and melanin. In explaining the epistasis of X over M in determining scale morphology, it may be less complicated to assume that morphology is a direct result of pigment-scale interaction. However, as one reviewer pointed out, in the absence of further information, independent determination is a better null hypothesis. In our model therefore, the X+ signal overrides M++ to redirect morphogenesis, and acts separately on genes involved with morphology and pigmentation as M is hypothesized to do.

This scheme of developmental genetic control is summarized by Figure 7. This diagram also shows the final genetically controlled decisions which occur after scale type is established which we have discussed above. For each branch, the gene dosages necessary for each state of a scale is indicated by plus (one gene dose) or zero (null).

Summary

Scanning electron microscopy reveals three morphological categories of wing scales in *Heliconius* butterflies. Type I, white or yellow scales, possess an obverse membrane between longitudinal ridges and lack conspicuous crossribs. Type II, melanic scales, have ladder-like, regular crossribs supported by trabeculae. Type III, red or brown scales, are characterized by crossribs which feature flutes and a thicker, more angular appearance. In hybrids, whose parents possess Type I and Type II scales on the hind wing bar respectively, the "bar shadow" scales which replace the yellow bar appear to be a slightly modified version of Type II scales.

Spectroscopic analyses reveal that yellow, red, and brown pigments are tryptophan derived 3-hydroxykynurenine, dihydroxanthommatin, and xanthommatin, respectively. White is a structural color expressed when yellow pigment is not present, while red and brown are different oxidation states of xanthommatin. Chromatographic evidence suggests the possibility that unstable forms of pigments in this pathway are maintained by association with peptides in the scale. Thus, although substantial color variation occurs within scale morphological types, it is chemically trivial. These observations are supplemented by evidence from the literature to develop an hypothesis for the relationship between genes, scale pigmentation, and scale structure (Figure 7).

Because of the variety of scale morphology and pigment chemistry within the Lepidoptera, it is not possible to assess the degree to which this scheme for *Heliconius* wing color pattern constitutes a model for other groups. However, it will be surprising if the *Heliconius* system described here turns out to be other than a variation on a theme common to all butterflies and moths. Indeed, a similar correlation of color and structure has been described for zygaenid moths (Burgeff and Schneider, 1979).

More generally, *Heliconius* wings may contribute to some of the unsolved problems of the genetics and development of tissue specific ommochrome pigmentation. This is because one can work with scale specific regulation of the pathway on the wings within species having distinctively patterned genotypic varieties or races, rather than rely on constitutive mutants.

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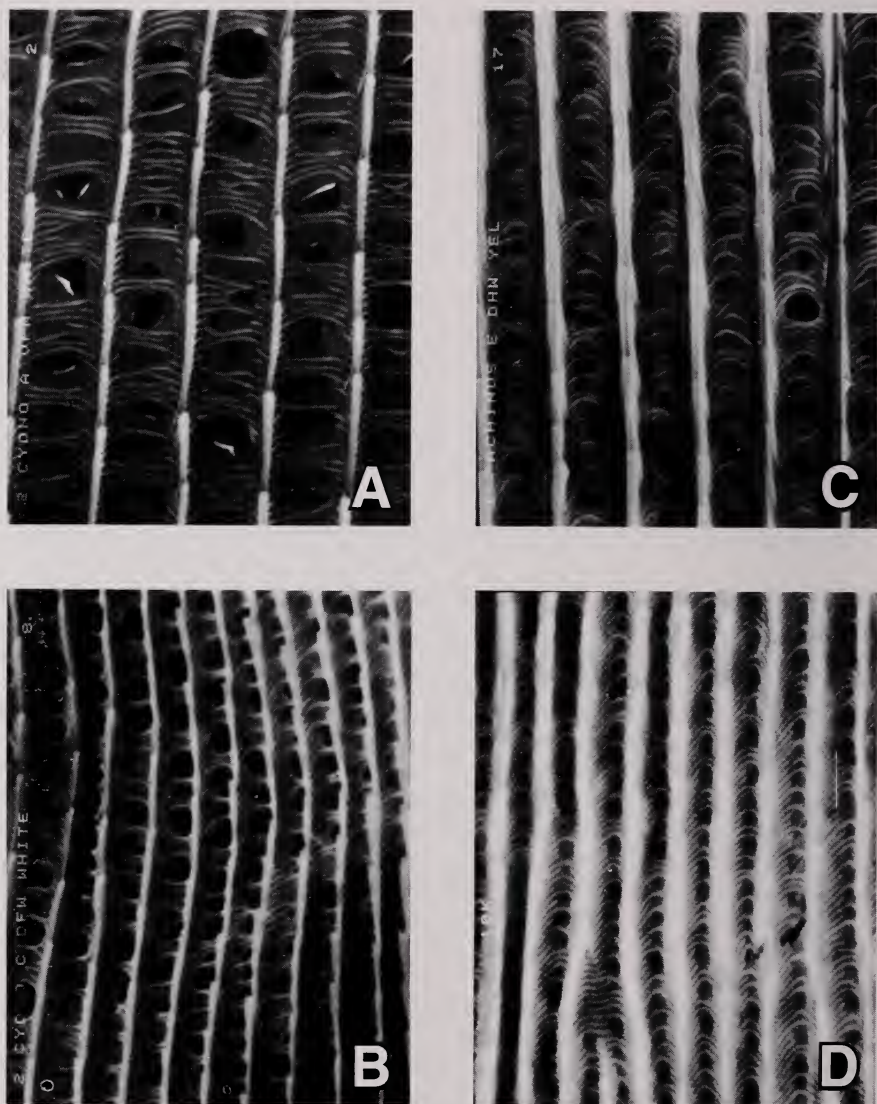
Fig. 1.   Type I, white or yellow scales. All cover scales viewed perpendicular to surface at 10k. A. White scale, ventral forewing, *H. cydno galanthus*. B. White scale, dorsal forewing, *H. cydno galanthus*. C. Yellow scale, dorsal hindwing, *H. pachinus*. D. Yellow scale, dorsal forewing, *H. pachinus*. Note on bottom left of D, where ridge spacing increases, obverse membrane of dorsal scale resembles that of a ventral scale.
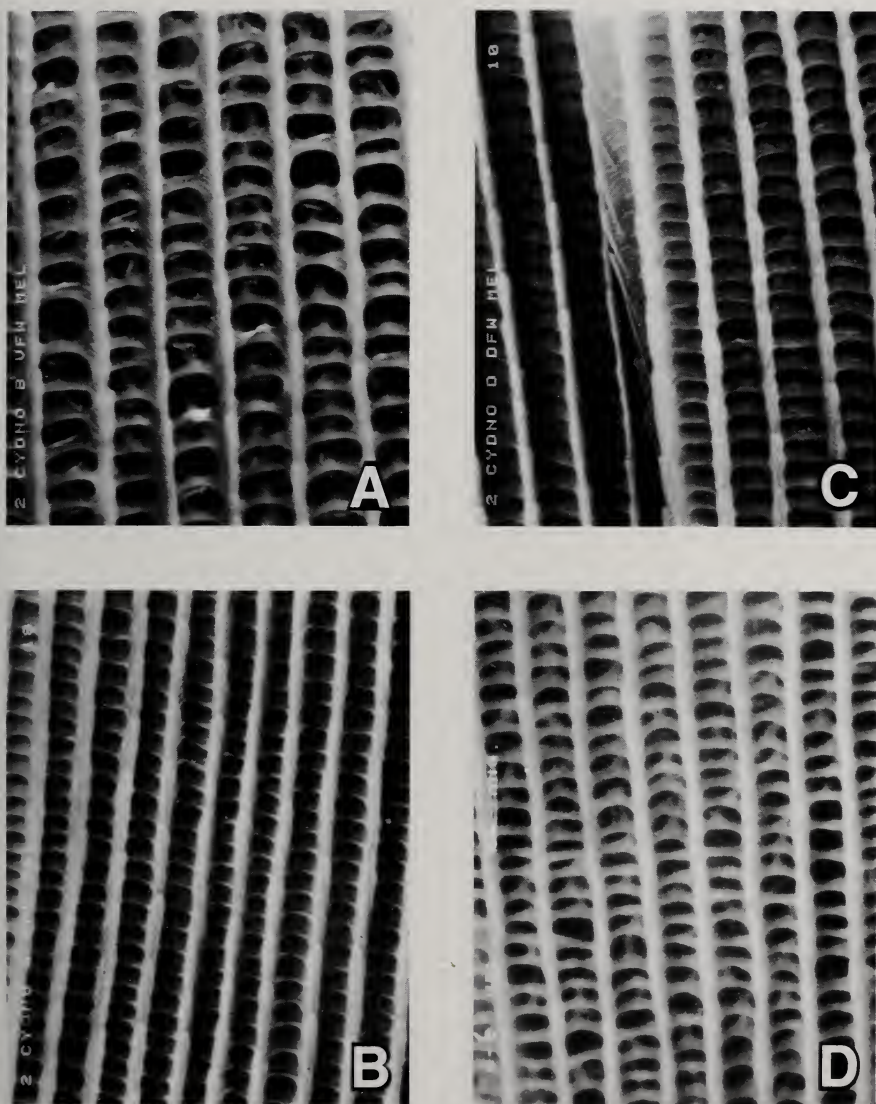
Fig. 2.   Type II, melanic scales. All viewed approximately perpendicular (±10°). A.
           Ventral forewing, *H. cydno galanthus*. B. Dorsal hindwing (shiny scale), *H.
           cydno galanthus*. C. Dorsal forewing (dull area), *H. cydno galanthus*. D.
           Dorsal forewing, *H. ismenius*.
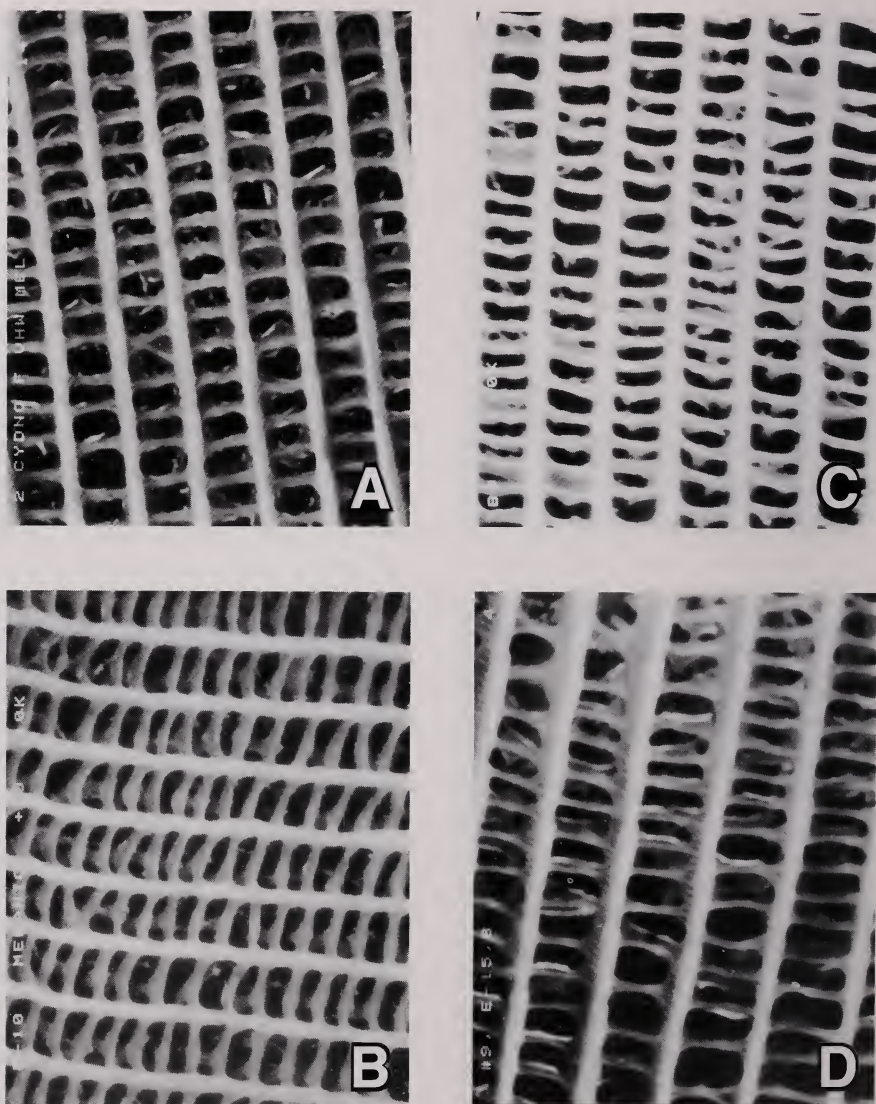
Fig. 3.   Type II, "shadow" scales. These ventral hindwing scales lie in zones of altered reflectance and are diagnostic of hybrids between forms with yellow hindwing bars X forms with all black hindwings. A. Shadow region of a *H. cydno galanthus* X *H. pachinus*, F1 hindwing. B. Non-shadow region of a *H. cydno galanthus* X *H. pachinus*, F1 hindwing. C. Shadow region of *H. cydno galanthus* X *H. pachinus*, F1 hindwing, D. Shadow region of *H. cydno galanthus* X *H. pachinus*, backcross hindwing.
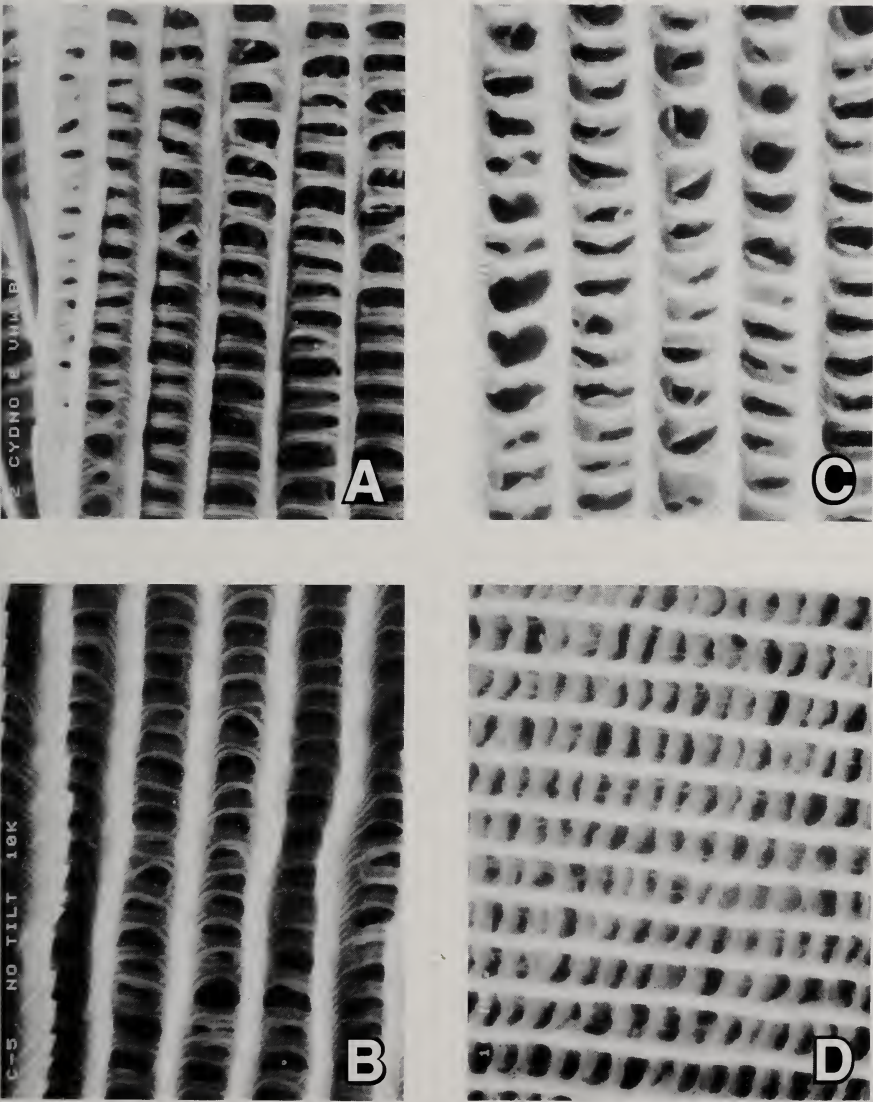
Fig. 4. Type III, red or brown scales. A. Ventral hindwing, *H. cydno galanthus* (brown). B. Ventral hindwing, *H. pachinus* (basal red spot). C. Ventral forewing, hybrid *H. cydno* with *H. melpomene* forewing band (brown). D. Dorsal forewing, hybrid *H. cydno* with *H. melpomene* forewing band (brown).
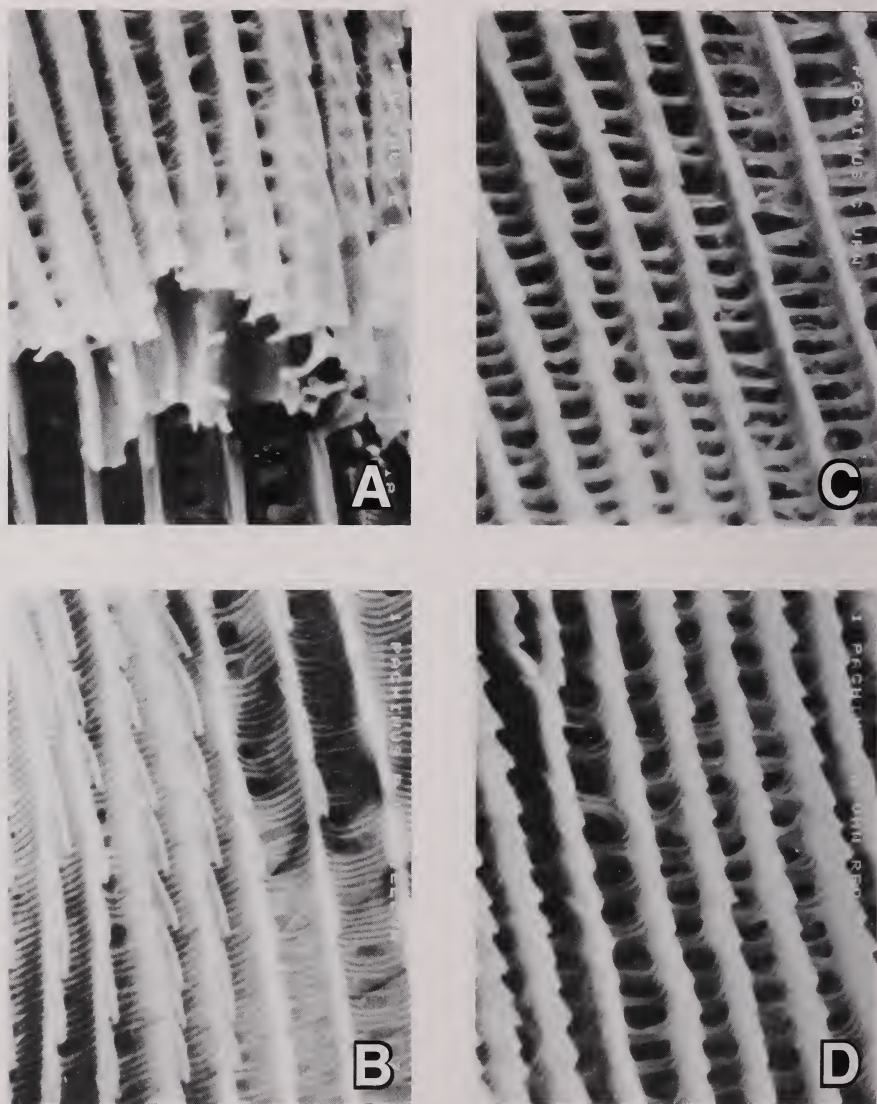
Fig. 5.   Angled views of various scale types (all of *H. pachinus*) showing scutes, all
at 10k. A. Dorsal hindwing, melanic, *H. pachinus*. B. Ventral hindwing,
yellow, *H. pachinus*. C. Ventral hindwing, melanic, *H. pachinus* D. Ventral
hindwing, basal red scale, *H. pachinus*.
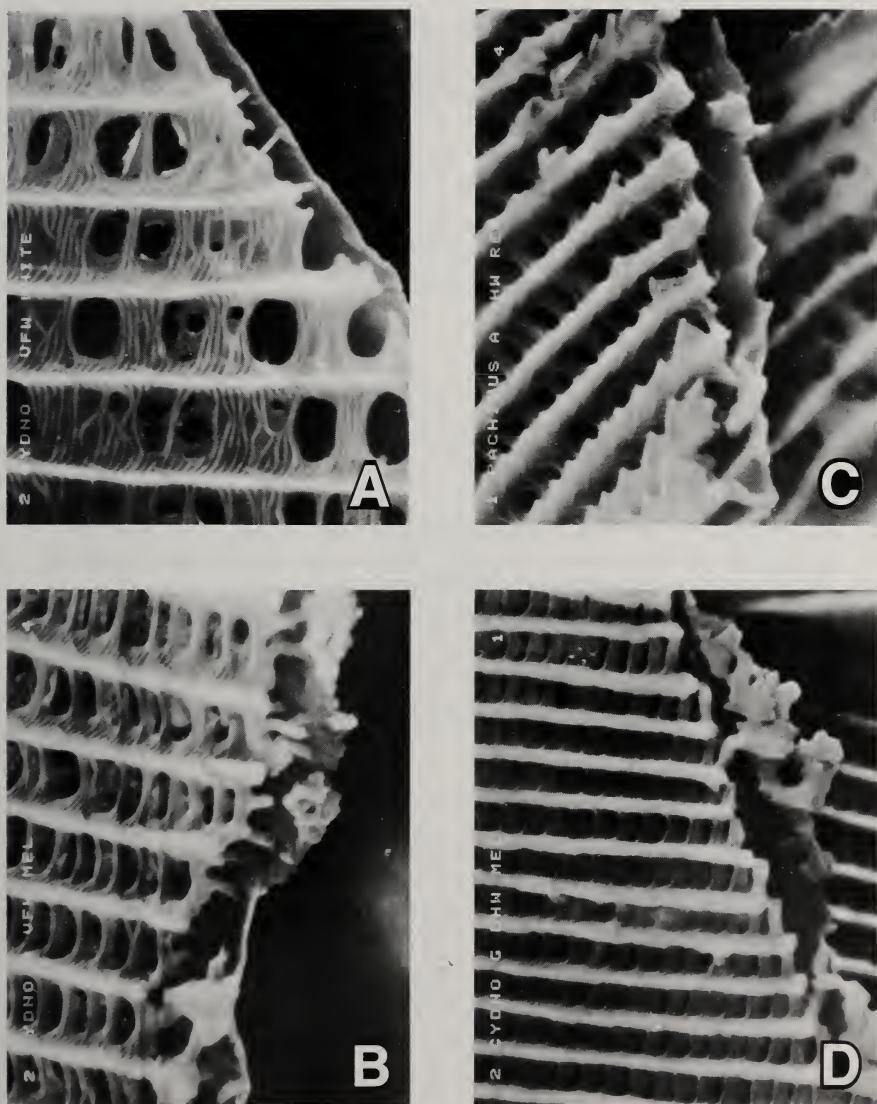
Fig. 6.   Cross sections of various scale types, all at 10k. A. Ventral forewing, white (Type I), *H. cydno*. B. Ventral forewing, melanic (Type II), *H. cydno*. C. Basal red spot, ventral hindwing, *H. pachinus*. Dorsal hindwing, melanic, *H. cydno*.
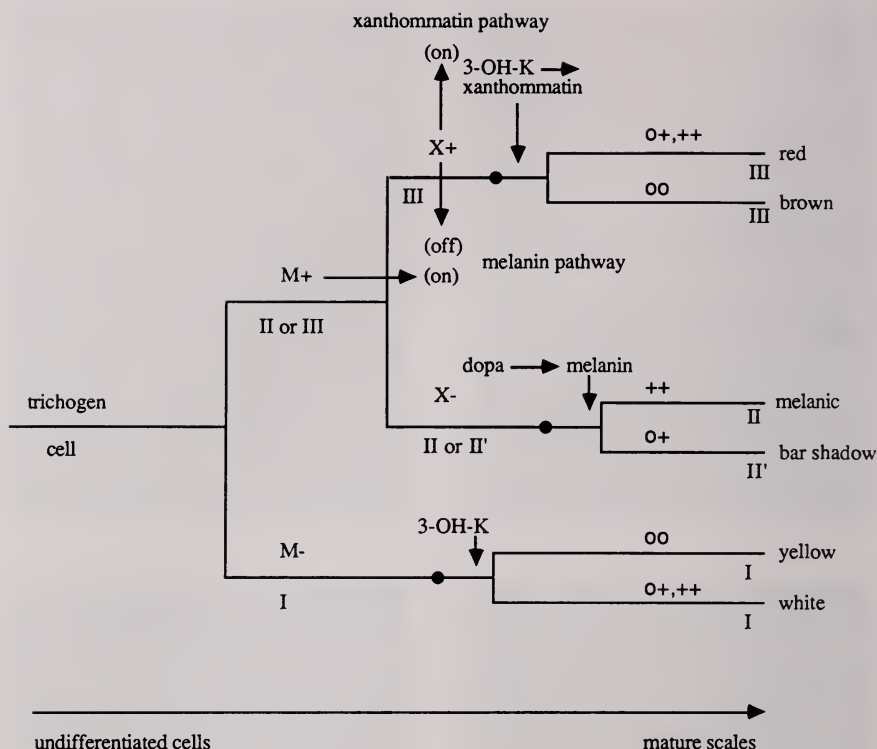
Fig. 7. Hypothetical scheme for genetic control of *Heliconius* wing scale develop-
ment based on morphological, chemical, and genetic information discussed
in text. Solid circle represents time that morphological characteristics of
mature scale begin to be established. M and X are selector genes regulating
morphological decisions and pigment pathways as shown. Effect of genes
which act within major scale categories are indicated on the final branches
of the diagrams in terms of doses (indicated by "+"). Type I scales vary in
terms of a gene which affects transport of 3-hydroxykynurenine (3-OH-K)
to the developing scale, one dose (o+) gives a white scale. Type II' scales
probably represent scales heterozygous for M (o+). Type III scales vary
according to a structural gene for a pigment binding peptide. One dose (o+)
stabilizes xanthommatin in its reduced state. (See text)

A mutant affecting wing pattern in *Parnassius apollo* (Linne) (Lepidoptera Papilionidae)

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Abstract. A mutant affecting wing pattern has been observed repeatedly and over a large number of years in a population of *P. apollo* from the upper Durance basin in France. It is dominant and morphologically modifies the postcellular region of forewings and the posterior part of hindwings, inducing a mask-like design in the former and obliterating the second eyespot in the latter. The frequency of the mutant in the population was 1 to 2% in the late 1970's. It has markedly decreased since.

Introduction

Scores of aberrations have been described in *Parnassius apollo*. However, no genetic work has been carried out although breeding of this species has been practised for some time. The main difficulty is obtaining mating in captivity. One of us has mastered the problem by hand-pairing. The method may permit production of a practically indefinite number of successive generations and thus genetic experimentation. The present paper, the first of a series with such experiments, involves a very spectacular aberration.

Materials and methods

Ova of either field-collected or bred females are obtained by placing females singly in a plastic-gauze cage of *ca* 1 liter (this device will be described with more details in a later paper). Oviposition is induced either by filtered sunshine or by a 60-100W incandescence bulb placed 20 to 50cm from the cage. In all cases, overheating *must* be carefully avoided. Ova are deposited singly or in small batches upon 1) a cellulose towel placed on the bottom of the cage, 2) foodplant fragments (*Sedum sp, Sempervivum*) which are not necessary to elicit laying, or 3) the cage walls. Regular feeding, once or twice a day, by a honey-water mixture (1:10) is essential. We have observed that old, almost exhausted wild females will recommence laying if carefully fed for several days. In all cases, it is

preferable to allow the females to lay for only a limited period (1-2 hours per day) and to keep them quiescent in a cool, shady place the rest of the time. Under these conditions, females can live 3 weeks or more and lay between 100 and 200 ova.

The ova generally diapause and are best refrigerated for at least 2 months at 0-4°C. However, a small portion of ova (1 to 5% in French populations, but much more in Spanish ones) hatch immediately and may be reared to adults by the end of summer (this observation implies the possibility of a potential partial second generation under natural conditions).

For breeding larvae, it is important to maintain a condition of cool or even cold air while using a heat radiating light: this condition can be satisfied using either sunshine or artificial light. It is possible to greatly accelerate caterpillar growth rate by continuous lighting, pupae being obtained within 10 days. Foodplants are various species of *Sedum*, according to their availability. *S. album*, of low vegetation, is especially convenient for starting young caterpillars, which do not spin silk and are consequently unable to climb over elevated plants. Some cultivated species are refused (*e.g. S. acre*) and may be toxic. The broods must be well ventilated, covering with gauze is unadvisable. Glass or plastic pans with appropriately high walls are convenient, since the walls are impassable barriers to the non-climbing caterpillars. Palik's method (1980), using cellophane walls, is more sensitive to use and can cause trapping of young larvae at the base of the plastic sheet. The offspring of a mutant female was lost in this way in 1980, which delayed the completion of the present study until 1984.

Copulation is easily obtained between bred individuals. The butterflies may pair freely even in a small cage (for instance a 50cm side cube), provided there is sufficient sunshine. However, hand-pairing affords the most reliable control of partner choice. We used Clarke and Sheppards's method (1953). Although *Parnassius* are markedly more difficult to pair than *Papilio*, success is generally complete when conditions are good and the operator skilled. Key factors are that males must be excited by sunshine and the females young. Although females can be kept ready for mating in a refrigerator at 4°C for several days, the freshest are best. Pairing lasts several hours (the couple is left still for this time under attenuated light). One male is capable of fecundating at least three females. In the first mating, a large, well formed sphragis is secreted; in the second one, this appendage is rudimentary and is absent in the third.

In all cases, however, fecundation is complete. We recall here that the sphragis is *not* a "laying pouch" as once stated, but a true "chastity belt", precluding further fecundation. The presence of fecund females with no sphragis or with a rudimentary one in the field is a strong indication that males can practise several successive matings. It is also possible that a female could be fecundated at least twice, first by an old male no longer able to secrete a sphragis and again by a young male. Such an event would be exceptional yet possible to check by counting the spermatophores present in the *bursa copulatrix*.

Results

FIELD OBSERVATIONS: For obvious reasons, we will not give the exact location where mutant individuals have been observed. It generally lies in the upper Durance basin, in french southern Alps. The habitat is a large set of rather smooth, sunny barren slopes, intermingled with mowed meadows, at *ca*. 1800m elevation. Few trees are

present, a condition quite probably due to forest destruction by man. The substrate is essentially formed by moraines and screes, with some thalwegs, not very accentuated, and a small stream. *Sedum* and *Sempervivum* are quite abundant and provide food for *Parnassius apollo*. The Parnassians themselves are very abundant over a large area. We carried out a mark-release-recapture study over a precisely defined small area of the flight locality. This experiment allowed us to estimate the population flying upon this area to 400-500 individuals (Napolitano, Cooke and Descimon, in preparation). The total area of the locality is much larger and extrapolation of the data allows to estimate the order of magnitude of the population being at least 10,000. By direct behavioral observation, it was seen that the butterflies move freely from one point to another over distances of at least one kilometer, as confirmed by the capture of marked individuals at distances of this order from their previous marking area. However, inhospitable zones circumscribe flight areas to some extent. In such inhospitable zones, individuals are casually seen, but are much scarcer by comparison. Other high density flight areas exist some kilometers away from the main one, but they are markedly smaller.

The first aberrant individuals were taken August 9, 1977, with three taken on one day. Only later on did we realize that, since the aberration was recurrent, it was probably due to mutation and that its frequency was worth further investigation. Still later, we discovered in the correspondence of the senior author a letter from Lucien Jean, who mentioned the capture of an "aberrant apollo" by another collector, Mr. Dreano, in the same locality. The letter was accompanied with a color slide which allowed us to verify that the female aberrant collected by Mr. Dreano belonged to the same type we found. This specimen had been captured around 1975.

The population has been followed regularly to 1981 and less intensively since 1982. We attempted to count all individuals seen to obtain a gross estimation of the mutant frequency (Table I). In most cases, counts were made by direct sighting, without marking correlation, so results must be considered approximate. At face value the frequency of the mutant decreased from ca. 2% to ca. 0.5% in five years. However, the 1985 capture of a normal female which produced mutant offspring indicated it had been mated by a mutant male and that the gene was still present in the population at that time.

A substantial fraction of the mutant individuals was secured, in particular 3 females for laying. Foolishly, we made the faulty assumption that the mutation was recessive, which would have implied that removing the thus supposedly homozygous individuals was not detrimental. This supposition was quite unfortunate, as we will see further.

It is worth noting that, when mutants were observed, they generally were in a group of 2-5 individuals flying in a restricted "pocket" surrounded by areas where none was to be found. It seems that this pocket correspond to the laying area of the mother female. Sometimes,

Table I. Number and percentages of *"Zorro"* mutant vs. "normal"
          phenotypes of *P. apollo*.

Year	Numbers of *P. apollo* observed		Percentage
1977	"normal" phenotype	*"Zorro"* mutants	
1977	*ca* 600*	12 (8 ♂, 4 ♀)	2.0
1978	*ca* 800*	14 (12 ♂, 2 ♀)	1.7
1979	1184**	7 (6 ♂, 1 ♀)	0.6
1980	136**	1 ♀	0.3
1981	*ca* 300*	0	0.0
1983	ca 200*	1 ♂	0.5
1985	*ca* 200*	1 ♂***	0.5
1987	*ca* 150*	0	0.0

* Individuals counted but not marked; in this case, we applied a correction coefficient keeping in account multiple captures and deduced from marking-releasing experiments.
** Individuals marked before being released.
*** Individual not observed, but existence deduced from the offspring of a "normal" female.

mutants were observed flying slightly more awkwardly than the normal butterflies and, in some cases, the degree of wing damage indicated they were less sturdy. Behavior was unaffected, but phenotype modification was discernible during flight to an experienced eye from a distance. When at rest in the absence of sunshine, *Parnassius* display a characteristical protective behavior. They open their wings in a horizontal plane and reveal their posterior eyespots. This display is accompanied by a kind of stridulation obtained by brushing the ventral face of hindwings with posterior legs (Descimon, 1965). The resultant noise resembles bruising silk and is perceptible to human ear from at least 1 meter. This behavior seems to occur in all species of *Parnassius*, including both *P. mnemosyne*, in which the hindwings do not have red eyespots, and the very ornate blue and red Himalayan species (F. Michel, pers. comm.). The mutants also display this behavior, but it's effect is entirely different to human observer's eye: attention is drawn from the hindwings, where the posterior eyespot is missing, to the forewings with their striking mask-like design.

BREEDING. In 1983, a male was secured and handpaired with a virgin female from the Lubéron (Vaucluse, France). A 1:1 segregation appeared in the offspring and, since the mutation had never been observed among thousands of butterflies in the Lubéron population, the mutation must be dominant. The gene was subsequently introduced into other stocks, including those from the Mercantour (Alpes Maritimes, France) and the Causse du Larzac (Aveyron, France). Further, a new mutant strain, isolated from the original Durance locality, was recovered

by chance. As already mentioned above, a normal female was collected amongst a group of normals. This female yielded mutants in a 1:1 ratio, which indicated that it had been fecundated by a heterozygous mutant male. In all mutant x normal crosses a 1:1 segregation appeared (table II). The only heterozygote x heterozygote cross (table II No.6) yielded a high proportion of mutant individuals. This result is puzzling. Indeed, the other crosses do not depart significantly from a 1:1 ratio, which precludes considering a superiority of heterozygotes over normal homozygotes. In No.6 cross, the excess of mutant phenotypes is not only too high to allow considering the possibility of homozygous mutant lethality (2:1 ratio, $X^2 = 9.6$, p‹0.01), but even to fit with the expected 3:1 ratio ($X^2 = 5.4$, p‹0.02). We, however, cannot draw conclusions from a single cross. Actually, the genetic composition of this brood was fairly heterogenous, which could give rise to "hybrid breakdown" phenomena and distort the ratios. In particular, we have indications that the Causse du Larzac population is peculiar; for instance, its ova are on the average twice as heavy as those from Alpine populations. The concerned cross was the only laboratory-bred of a series of identical parentage which was used to make an experiment of founding an artificial population of *P. apollo* on the Sainte Baume mountain, where it is absent. Now, this experiment, which involved the deposition of 1,000 ova upon favorably

Table 2.   Results of crosses with *"Zorro"* mutant of *Parnassius apollo*.

Number of the cross	Parents	Offspring "normal"	"Zorro"
1	♂: *"Zorro"* from *"Zorro"* ♀ x "normal" ♂ from Mercantour ♀: wild, normal, Briançon	21 (9 ♂, 12 ♀)	24 (9 ♂, 15 ♀)
2	♂: wild, "normal", Causse du Larzac ♀: *"Zorro"* from *"Zorro"* ♀ x wild "normal" ♂, Lubéron	16 (7 ♂, 9 ♀)	17 (10 ♂, 7 ♀)
3	♂: *"Zorro"* from a "normal" ♀ caught in the wild ♀: "normal" from all-normal F_1 from the original locality	40 (14 ♂, 16 ♀)	39 (19 ♂, 10 ♀)
4	♂: wild, "normal", Mercantour ♀; *"Zorro"* from 3	7	7
5	♂: wild "normal", Lubéron ♀: *"Zorro"* from 3	7	12
6	♂: *"Zorro"* from 2 ♀: *"Zorro"* from 2	2	28

sited foodplants, has been unsuccessful. Moreover, the mortality in the brood was high (only 30 adults from 110 ova), in spite of having been pampered. More experiments are needed but, unfortunately, they are at present impossible.

MUTANT GENE EXPRESSION AND VARIATION. The average mutant phenotype is represented on figure 1 (A: male, B: female). On the forewings, it is the region posterior to vein 7 which is modified: the discal spot is elongated distally into a point following vein 7. Basally, this spot shows a tendency to be connected to the median (discocellular) spot of the cell by two black streaks following the anterior and posterior limits of the cell. The marking gives mutant butterflies a striking aspect, as if they bear a black mask. The postdiscal row of spots is shifted distally and partly obliterated in 5-6 and 6-7 intervals. No obvious modification is to be noticed in 2-3 and 3-4 intervals, but the spot of the 1b-2 interval, very characteristic of the species, is conspicuously shrunken and divided into two parts by 1c rudimentary vein. On the hindwings, the anterior eyespot is absolutely unaffected, while the posterior one, which lies in
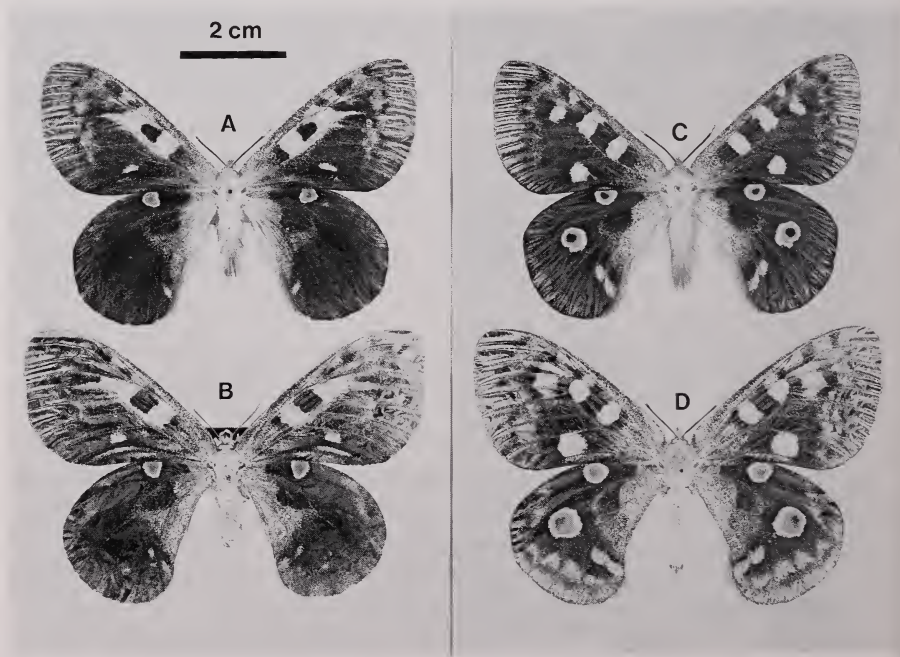
Fig. 1.   "*Zorro*" mutation of *Parnassius apollo*.
          A - male mutant, wild collected, 2 VIII 78.
          B - female mutant, wild collected, 14 VIII 78.
          C - male, normal phenotype, same locality, 28 VII 79.
          D - female, normal phenotype, same locality, 6 VIII 78.

3-4 and 4-5 intervals, is extremely modified. It is dissociated into two parts, as if a factor following vein 4 inhibited the formation of the eye-spot pattern. The series of anal spots in 1b, 1b-2 and 2-3 is diminished but still present. Premarginal black scales lunules and marginal hyaline band are slightly displaced basally.

It is rather obvious that such a remarkable mutation deserves a name. Here we meet with a problem which has not been considered seriously for Lepidoptera. In species such as *Drosophila melanogaster*, which has not been plagued by a crowd of aberrational names given by mere "curios" collectors, matters are clear. Mutational names are indispensalbe working tools, with simple and clear terminological rules. In all animals, the practice of giving latin names to any infrasub-specific form has been rejected by the International Commission of Zoological Nomenclature. We believe that this does not preclude using non-linnean names which would follow the rules of genetic nomenclature in the case of variants which have in fact been studied genetically. The controversial situation arises in the case of "classically named aberra-tions" or morphs which later prove to be mutants. At first sight, it seems advisable to retain the old names. However, some cases would be quite puzzling; for instance, for the white female of *Colias croceus*, should we use the old name of *"Helice"* given by Hübner or, following the American authors, the generic name of *"Alba"*, which assume that all white female mutants are homologous? In any event, we propose here the *mutational* name of *"Zorro"* for the described variant of *P. apollo*. Names that we would have preferred, such as *mephisto* or *diabolicus*, have been already given to *Parnassius* variants or subspecies; otherwise, the selected name will recall that nomenclature need not be such a serious topic, after all...

Field-collected, as well as bred examples of *"Zorro"* display variability. We noted above this is not due to incomplete dominance. The argument is reinforced by the fact that the probability of occurrence of homozygous mutant individuals in natural populations is very low (practically equal to variant frequency, that is 2 to 0.5 percent). Moreover, when variation is observed within bred individuals, it must be due mainly to interaction of the mutant gene with its genetic background, since rearing conditions were kept relatively constant. Fig. 2 shows some of this variability; individual 1 is among the least accentuated and 2 among the most. There is also an interaction with sexual dimorphism. If venation is not markedly modified on forewings, some striking abnormalities may be observed on hindwings. In all cases, a rudimentary cell is present at the outer extremity of the cell between M1 and M2 normal veins, but much more spectacular modifications can also occur: the cell is open between M1 and M2; M1 is often branched and in some cases a complex system of supplementary cells is formed. These modifications are often assyme-trical. Figure 3 gives an idea of these atypical vein patterns.
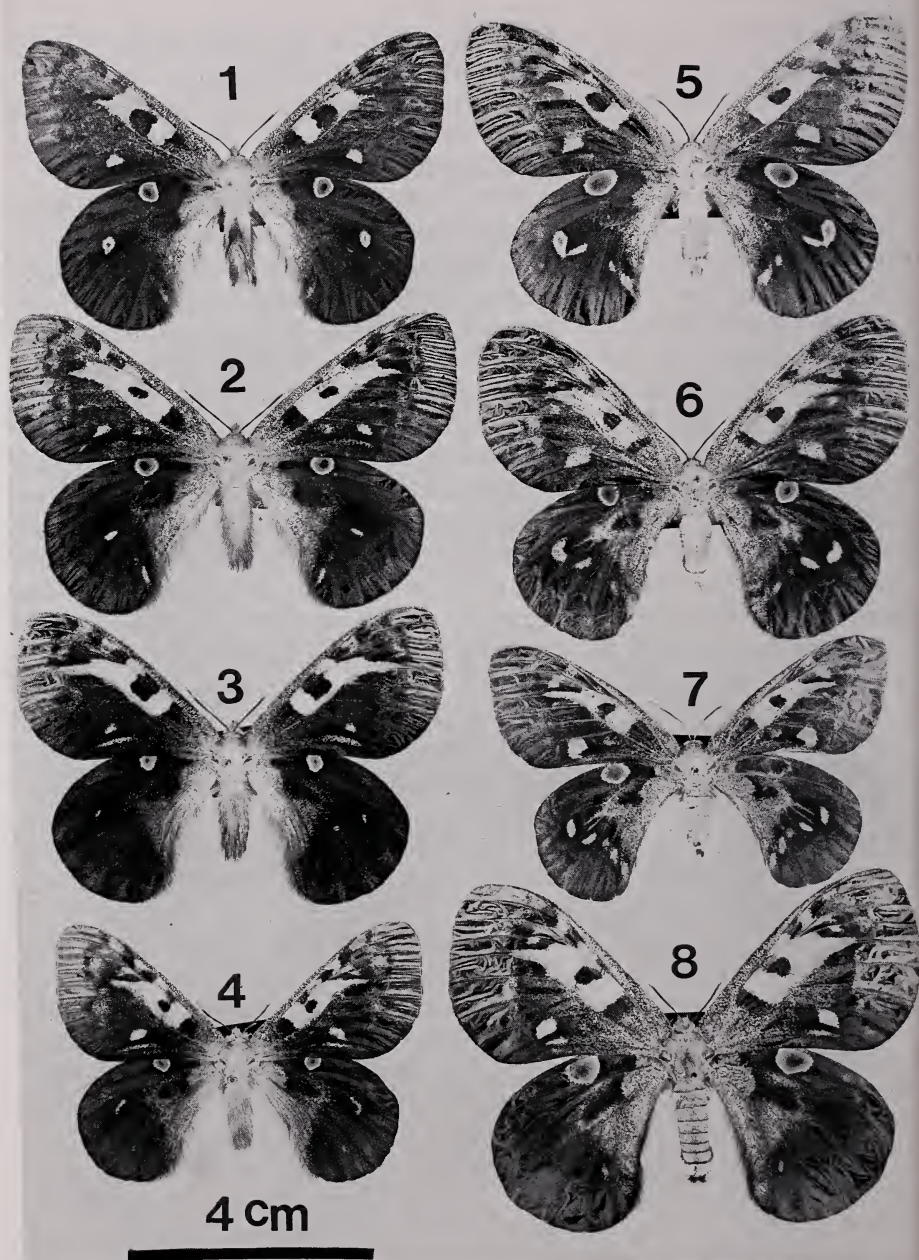
Fig. 2. Variation in the expression of "Zorro" mutation in *Parnassius apollo*.
   1 - male, wild, 13 VIII 77.
   2 - D°, D°, 27 VII 78.
   3 - D°, D°, 14 VIII 78.
   4 - D°, D°, 28 VII 79.
   5 - Female, D°, 2 VIII 78.
   6 - D°, D°, 10 VIII 77.
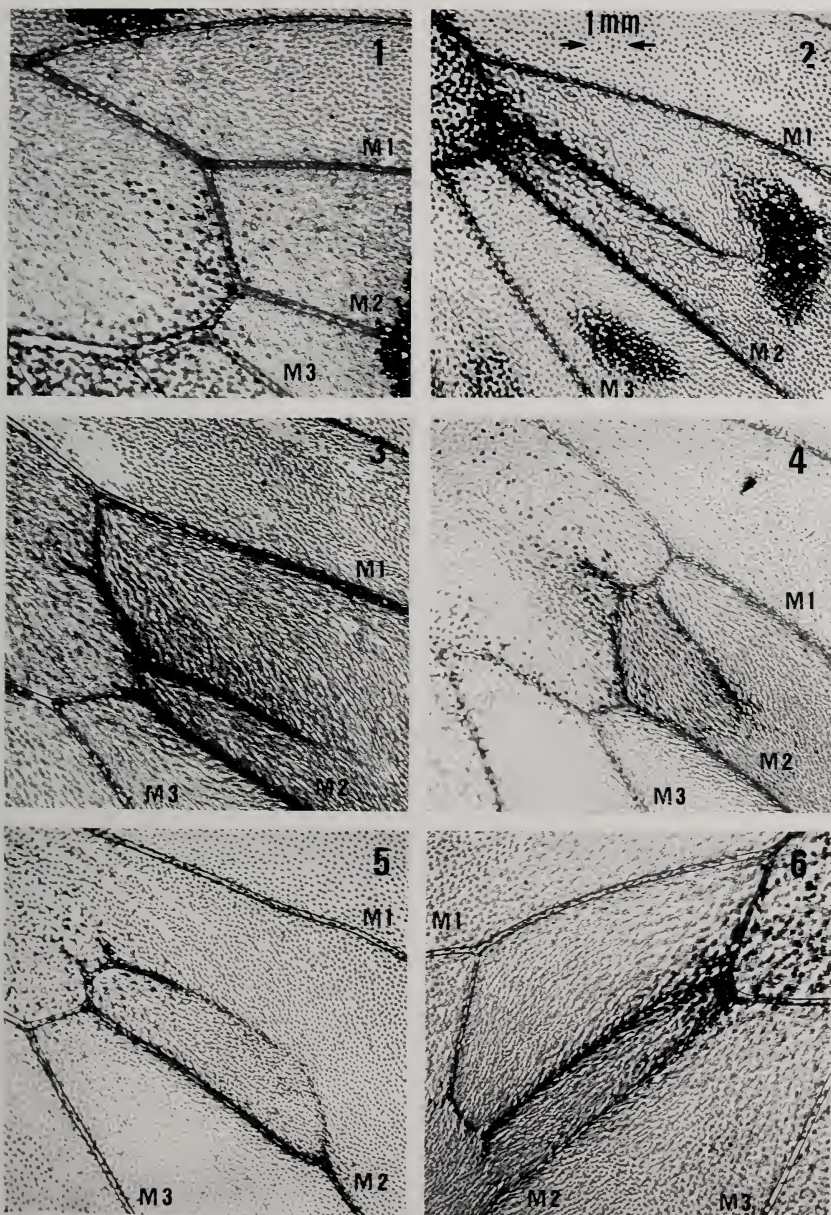   7 - D°, bred (Brood Number 1, see table II).
   8 - D°, D° (Brood Number 2)

Fig. 3.   Abnormalities of venation in "Zorro" mutation of *P. apollo*.
1. Normal female.
2. "*Zorro*" female (n° 6 of fig. 2), with supplementary distal vein.
3. D°, brood n° 6: supplementary distal vein plus intracellular rudimentary vein.
4. D°, male, brood n° 6: D°, with different branching.
5. D°, female, brood 5: supplementary cell with atrophy of normal cell closure.
6. D°, female, brood 5: supplementary distal cell.
All figures represent right hindwing in the region where median veins (M1, M2, M3) take rise from the cell, except n° 6, where it is left hindwing which has been photographed.

Discussion

From a morphogenetic point of view, *"Zorro"* is one of the most striking aberrations in *Parnassius*. A thorough survey of the previous described forms in available literature (*e. g.* Bryk, 1935, Eisner, 1966) did not reveal any close equivalent. It may be remarked that, in both pairs of wings, the mutation modifies only the posterior half, while the anterior one remains unaffected. Pattern and venation are most perturbated at the suture between the imaginal disk compartments which, according to the studies of Sibatani (1981), follows the axis of symmetry of the cell and the corresponding distal part of the wing. It is obvious that *"Zorro"* could provide a choice tool for the study of the development of wing pattern, using for example the methodology of Nijhout (1985). Unfortunately, it is probable that practical difficulties would render such a study rather difficult.

From the point of view of evolutionary genetics, the history of this mutation appears clear. It arose once, at one locus of one individual of the population. It is more difficult to understand how its frequency reached 1 or 2 percent. If we assume the size of the population, previously estimated to roughly 10,000, the original frequency must be around 0.5×10^{-4}. To reach the 10^{-2} frequency observed in 1977, the *"Zorro"* allele therefore must have been multiplied by 200. The simplest explanation would be to assume the population had been reduced to few individuals in at least one year, the mutation having been preserved by chance (or having appeared) during the time of the population contraction. Further, its frequency would have been amplified in parallel to the population increase. We can provide some observational support to this hypothesis: the senior author and his brother Robert Descimon have collected and observed butterflies very regularly in the region until the present time and *P. apollo* was noted as very scarce at the end of the 1960's. It is further noteworthy that the *"Zorro"* mutation was not observed in the locality where it was later discovered. Many *P. apollo* were seen during early 1960's.

Could selection have played a role in the variation of the frequency of the mutation? From 1977 to 1981 *"Zorro"* has obviously decreased. It is very unfortunate that we did not surmise that this aberration could be a dominant but postulated it was a recessive, with a gene frequency of about 0,14, providing the observed "homozygote" frequency of 2 percent. Under these conditions, we incorrectly believed that securing and killing some individuals was not detrimental. Actually, we introduced a massive selection coefficient, "destroying our own subject of study", according to the accurate expression of Dubois (1983). Fortunately, only a portion of the population was screened and the mutation was not eradicated in totality. The most distressing consequence of this thoughtless action is that we are now hindered from drawing conclusions. Would *"Zorro"* frequency have decreased anyway? It has been clearly observed that the mutants appear a trifle handicapped in flight activity.

At the larval stage, however, no disadvantage appears to exist; in one brood, an excess of mutants has been observed. The experiments should be repeated with a larger sample. The modification of wing pattern does not obviously impair its deterrent effect. To human eye, it is even more frightening! Therefore, we may not rule out the hypothesis that the mutation was slowly increasing its frequency when we clumsily intervened.

Although rather unusual, the dominance of "*Zorro*" seems to be best interpreted in terms of physiological genetics. The observed variation in expression does not seem related to overdominance but to the interference with the entire genotype. It would not be relevant to hypothesize that the mutation should have become dominant after a process of "evolution of dominance" (Ford and Sheppard, 1966), since none of the conditions for it appear here.

We have planned to "repair our fault" by breeding and releasing mutant individuals (with, of course, no mixture with foreign strains) into the locality. To do so, we would introduce yet another perturbation into the population. The best would be to proceed but with seriously controlled and monitored conditions. Only accidental difficulties have delayed this operation. We also intend to undertake again experiments of creating artificial populations like the one previously mentioned, which has been probably unsuccessful. Such attempts (which are debatable if not carefully designed) have proven successful and quite instructive in some cases (Descimon, 1976, Holdren and Ehrlich, 1981).

Cases of decreasing mutation frequency in natural populations by collecting are already known. The most striking is probably the "*honnoratii*" form of *Zerynthia rumina* in the region of Digne (Alpes de Haute Provence, France). The problem, which has elicited some row in the local press (with ridiculously exaggerated considerations, especially about the prices fetched on butterfly market) led to the promulgation of a law forbidding all insect collecting in the concerned department. Notwithstanding the inadequacy of enforcing the law, it is almost certain that it has improved the chance of maintaining the mutant gene. *Z. rumina* "*honnoratii*" has been observed in recent years (P. Bonnet, pers. comm.).

We believe that, for "*Zorro*" as for "*honnoratii*", the best protection is to breed and distribute them to collectors, who would be deterred from painstakingly seeking for them in nature. Further, lowering the venal value would render the "black market" less likely. One would pass from "hunting and gathering" to "farming". We strongly suggest "desperate hunters" not only search for *new* aberrations, but breed them, obtaining at the same time not only fine collection items, but genetic information. Such a practice has been frequent for some time in England - it must be generalized.

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Mimicry by illusion in a sexually dimorphic, day-flying moth, *Dysschema jansonis* (Lepidoptera: Arctiidae: Pericopinae).

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Abstract. Sexual dimorphism and development in *Dysschema jansonis* (Butler, 1870) are discussed, and wing patterns of females and males are compared with those of their models, female *Parides* spp. (Papilionidae) and transparent-winged ithomiine nymphalids, respectively. Two questions are addressed: Why does *D. jansonis* not display more accurate mimicry? How does *D. jansonis* create the illusion of mimicry?

Introduction

Species of the genus *Dysschema* Hübner, 1818 are well-known examples of diurnalism in moths (Klots & Klots, 1959), and sexual dimorphism of wing pattern and color in Lepidoptera (Watson & Whalley, 1975). They are presumed mimics of unpalatable butterflies of various groups (Fisher, 1958; Gilbert, 1984; Watson & Whalley, 1975), and it is possible that they themselves are unpalatable, Müllerian mimics. The following remarks concern *D. jansonis* in the Republic of Panamá.

Sexual Dimorphism

In general appearance, males and females of *D. jansonis* are strikingly different (Figure 1). However, a careful inspection reveals that the same wing pattern elements are present in both sexes. The dorsal forewings of the two sexes are quite similar, except that the pattern shows slightly more contrast in males. The hind wing pink forms a large blotch at the posterior margin in females, but is reduced to a tiny dot or is absent in males. The dorsal yellow, restricted to a round mark near the anterior margin of the hind wing in females, occupies the basal three fourths of the wing in males. In both sexes, the ventral side closely resembles the dorsal side except that in the male the forewing markings are more pronounced on the ventral surface than on the dorsal, and in

Fig. 1.   Left column, from top: *Dysschema jansonis* males (D, YCF), (D, WCF), *Oleria rubescens* (D), *D. jansonis male (V, WCF); Middle column, from top:* Eurytides ilus *(D), Papilio anchisiades (D);* Right column, from top: *D. jansonis* females (D), (V), *Parides arcas* female (D).
Figure codes: D = dorsal, V = ventral, YCF = yellow color form, WCF = white color form.

the female the ventral forewing bears a yellow band that is only faintly evident on the dorsal side.

Sexual Differences During Development

Five males and six females of *D. jansonis* were reared from a clutch of 13 eggs laid by a single female, 10. XI. 1982 during daylight hours, on the underside of a leaf of *Spiracantha cornifolia* (Compositae) at the Summit Observatory in the Canal area of the Republic of Panamá (Aiello Lot 82-62). All 13 eggs hatched on 22. XI. 1982. One larva died in its first stadium, another died as a late instar, but the other 11 completed development to adult.

Females passed through eight larval stadia and required 72-80 days ($\bar{x} = 75.83$ days, $s = 3.19$) to complete development from egg to adult, whereas males had only seven larval stadia and completed development in 66-69 days ($\bar{x} = 67.60$ days; $s = 1.14$). The late larva that died, did so on day 69 as a ninth instar. One can only guess at the sex of that individual; possibly it was an exceedingly small male who had difficulty achieving the minimum weight necessary for pupation.

Early stadia were synchronized; all 13 eggs hatched on the same day, and molting occurred synchronously through stadium six. Larvae in the first through third stadia aggregated, and fed by scraping the upper leaf surface either while strung out along one edge of a leaf, or while lined up parallel to one another to form a feeding front. Fourth

instars began to show conspicuous size variation, and from then on were solitary and ate whole leaf instead of scraping the surface. Molts to seventh and eighth stadia were asynchronous; the molt to stadium seven occurred over two days, and that to stadium eight took place over four days. Following the molt to stadium seven, all larvae were transferred to separate cages and given individual numbers. Six individuals that were larger than the others were numbered 1-6, and all proved to be females; the smaller larvae (numbered 7-11) turned out to be males.

Adult eclosions in both sexes took place between 1500 and 1700 hours.

Mimicry in Females

Dysschema jansonis females resemble females of the aposematic butterflies *Parides* spp. (Papilionidae), when in flight. Like *Parides* (Figure 1), they have yellow and pink markings against a black background. However, in *Parides* the yellow is on the forewings and the pink is on the hind wings, while in *D. jansonis* both color elements are located on the hind wings. This seemingly important discrepancy does not detract from the mimetic effect when the moth is in flight; the human observer, at least, sees the rapidly fluttering moth as a fast-moving *Parides*. The illusion is made possible partly by exposure of the yellow band, on the underside of the forewing, during the high wing-stroke flight of this moth, and partly by the fact that when the wings are spread they are somewhat translucent, and the underside yellow shows through them from above.

There exist a number of other *Parides* look-alikes with much more convincing mimicry. In Panamá, *Eurytides ilus* and *Papilio anchisiades* (Papilionidae) (Figure 1) have the yellow on the forewings and the pink on the hind wings as does *Parides*. A probable explanation for *D. jansonis*'s "imperfect" mimicry of *Parides* can be found in the resting posture of this moth. Both sexes rest, with the forewings covering the hind wings, on foliage or bark where they blend with their background or resemble a bit of dead leaf. A yellow band or large white area on the dorsal forewing might interfere with this resting-posture crypsis. *D. jansonis* has overcome this constraint by employing mimetic illusion, and as a result possesses two distinct modes of visual protection.

Another example of mimicry by illusion can be found in the nymphalid butterfly *Consul fabius*, which resembles a dead leaf when at rest with its ventral cryptic pattern showing, and a tiger-striped *Heliconius* when in flight with the dorsal pattern exposed. The illusion occurs when *C. fabius* flies in sunlight and the dorsal mimetic pattern shows through the wings from below as well (DeVries, 1987).

Mimicry in Males

Dysschema jansonis males resemble various genera of transparent-winged ithomiine nymphalid butterflies (Figure 1). Although scaled,

the wings of *D. jansonis* males appear transparent when in flight, an illusion made possible by the fact that dorsal and ventral surfaces are identically patterned, and enhanced by exposure of the strongly marked ventral forewing during flight. In addition, when the wings are spread, the paler areas are translucent, a fact which can be demonstrated by holding a pinned specimen to the light. Males' fluttery flight further contributes to the ithomiine resemblance.

When at rest, with the forewings covering the hind wings, transmitted light and wing pattern contrast are reduced, and the moths blend well with mottled bark or dried leaves. Reduced contrast can be demonstrated by placing a pinned specimen over a dark background.

Male Color Dimorphism

Some males have white, instead of yellow, hind wings, and while it has been supposed (Druce, 1884; Hering, 1925) that the two forms are mere color variations of the same species, no evidence has been presented until now. Of the five males reared from the single clutch of 13 eggs, three were the white color morph and two were the yellow. Presumably both are ithomiine mimics; transparent-winged ithomiines include species with clear, and species with yellow-tinged wings.

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"Black-Light" Induction of Photoperiod-controlled Diapause Responses of the Viceroy Butterfly, *Limenitis archippus* (Nymphalidae)

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Abstract. The nearctic viceroy butterfly, *Limenitis archippus* (Cramer), is a typical long-day insect. The 2nd and early 3rd instars are photosensitive. Half-grown larvae respond to short-day (autumn) photoperiod by constructing hibernacula and entering diapause. Long-day photoperiod induces rapid growth and direct development. Previous experiments testing this facultative response have used fluorescent bulbs emitting both UV and visible light (320-700 nm). However, both diapause and direct development can be induced in larvae exposed to "black-light" photoperiod regimes containing mainly the near UV (violet) and UV portions of the spectrum (320-436 nm). The stemmata and dorsolateral abdominal saddlepatch areas of the 2nd and 3rd instar larvae represent possible photoreceptors for mediating these responses.

Introduction

Many temperate insects respond to changes in daylength through hormonally regulated physiological mechanisms influencing direct development or diapause (Lees, 1955, 1960; Danilevskii, 1965; Andrewartha & Birch, 1973, Saunders, 1976, 1977; Tauber & Tauber, 1973, 1976; Beck, 1980). Typical long-day insects exhibit diapause when exposed to short daylength ($<$ 11 hr light per 24 hr day) but show direct development under longer photoperiods. Such environmentally induced responses are termed facultative. The photosensitive stages vary between species, and may involve eggs, larvae, pupae, or adults (Wigglesworth, 1970, 1972). Such responses exhibit variability within and between broods in a single species. Temperate insect strains from different latitudes or altitudes, exhibit similar variation. (Tauber & Tauber, 1972; Beck, 1980; Ujiye, 1985). Diapause is related to insect endocrine control and metabolism (Gilbert et al, 1960; Harvey, 1962; de

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Wilde, 1965; Harvey and Haskell, 1966), and is under polygenic control in most species. Recently, a dual system involving photoperiod and temperature for regulating circadian rhythms and diapause has been proposed (Beck, 1977; Neumann & Krüger, 1985).

Facultative diapause in the nymphaline butterfly *Limenitis (Basilarchia) archippus* (Cramer) has been studied by Clark & Platt (1969), Hong & Platt (1975), Frankos & Platt (1976), and Williams & Platt (1987). This species enters larval diapause when exposed to short-day photoregimes at room temperature. Second and early 3rd instar larvae respond to photoperiod over a seven to ten day period. Larvae preparing to diapause grow more slowly than their long-day siblings. Those reared in either continuous light or in complete darkness exhibit nearly 100% mortality (Platt, pers. obs.). Diapause initiation and termination take place while development is arrested in the 3rd instar. Thus, the diapause responses of *Limenitis* are not complicated by developmental processes associated with metamorphosis, as they are in other species which diapause as pupae.

Complex innate behavior precedes larval diapause and can be conveniently studied in short-day larvae. This behavior is genetically based (Clark & Platt, 1969; Hong & Platt, 1975), but is expressed only under short-day conditions. Short-day larvae grow slowly and construct hibernacula (overwintering chambers) from the basal portions of poplar (*Populus spp.*) and willow (*Salix spp.*) leaves (*Salicaceae*) on which they feed. These tubular structures are made by chewing the leaf in a characteristic manner, and then covering the remaining basal leaf surfaces with silk to form an enclosed curving tube which remains open at its outer (distal) end. The hibernaculum is attached to the foodplant twig with a substantial silk girdle formed around the leaf stem and surrounding next season's bud (Edwards, 1884; Scudder, 1889; Weed, 1926; Klots, 1951). The hibernaculum remains attached to the plant throughout the winter months following leaf drop. Short-day larvae crawl into these chambers prior to diapausing. Physiological changes such as water loss and glycerol accumulation accompany diapause (Frankos & Platt, 1976). Diapause onset can be reversed by switching short-day larvae to long-day conditions (LD 16:8), even after hibernaculum formation and entry have occurred. However, the reciprocal transfer of 2nd and 3rd instar larvae (from long-day to short-day photoregimes) usually results in larval death (Clark & Platt, 1969).

Few papers have addressed the wavelengths (colors) of light which influence insect diapause. Beck (1980) states that the most effective wavelengths are between 400-550 nm for most species. Bünning and Joerrens (1960) found that blue light induced diapause in *Pieris*

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[2]Larvae were not reared in photochambers containing the insect "black-light" bulbs, because plants placed in these chambers wilted within 12 hrs, and their leaves dried up. This evidently resulted from the light quality emitted by these particular bulbs.

brassicae L. (Pieridae) during early photophase, but that red light promoted diapause later in the diel photoperiod cycle. However, Beck (1980) criticized their conclusions, which he believed could be explained more simply by assuming that the red light regime was equivalent to total darkness in their experiments. The spectral limits for diapause induction in *Limenitis* have not been previously determined.

In this paper we show that *Limenitis* larvae exhibit normal diapause reponses when grown in photochambers containing fluorescent "black-light" bulbs emitting a partial spectrum of violet-blue and ultraviolet (UV) wavelengths. UV light is known to be an important spectral component of many insects, especially Lepidoptera (Silbergleid, 1979). Clark & Platt (1969) suggested that the dorsolateral grey-white abdominal saddlepatch of young larvae may represent a photosensitive region. This pale saddlepatch makes the small larvae cryptically patterned, and helps them resemble bird droppings when at rest in curved positions on the leaves and twigs of their foodplants. The stemmata (ocelli) of larvae also are known to possess UV receptors (Ichikawa & Tatda, 1982).

Materials and methods

All larvae were reared from eggs in light-tight wooden photochambers (61 × 61 × 42 cm inside dimensions) at room temperature (25 ± 2°C). The inside walls of the chambers were painted a non-fluorescent flat white. Experimental chambers contained single 15″ G. E. fluorescent "black-light" bulbs emitting a partial spectrum between 320-436 nm [so-called "poster lights" Fig. 1A)]. The quality of light emitted by these bulbs is a deep, dim violet. The "poster light" bulbs are dark purple in color, but the wavelengths emitted are not the same as those of "black-lights" used commonly to attract and trap insects (Fig. 1B)[2]. Control chambers contained G. E. cool white fluorescent bulbs identical in size and wattage, which emitted wavelengths throughout the visible spectrum and some UV as well (Fig. 1C).

The emission spectra were measured as follows: Light from each type of source passed through an Oriel computer-driven monochromator to a photomultiplier (PM) tube (Hamamatsu R-928) through an evacuated quartz window. The lamp's output was measured at each nm from 300-600 nm by averaging the digitized photocurrent of the PM tube (200 measurements per nm), without correction for the spectral response curve of the PM tube. These data were subsequently normalized to the peak value. The different emission spectra obtained from the three kinds of fluorescent tubes are shown for comparison in Fig. 1.

The larvae were reared on rooted cuttings of weeping willow (*Salix babylonica* L.) in moist conditions using long-day (LD 16:8) and short-day (LD 8:16) photoperiods. The onset of photophase occurred at 8:00 a.m. EST in all chambers. A total of 81 larvae was reared during the experiments.[3]

Individual larvae were taken from stock cultures maintained in the laboratory, or were collected as diapausing larvae in hibernacula. Eggs from three *L. archippus* females, which had been hand-paired using Platt's (1969) method, were used in the induction experiments (Table 1). Eggs from each brood were

divided evenly between the control and experimental conditions. Diapause termination studies were done using overwintering *L. archippus* larvae obtained by collecting hibernacula from the vicinity of Conowingo Dam, Cecil Co., Maryland (Table 2). Some wild-collected larvae had been parasitized by wasps, as noted in the table.

Photochambers were checked daily to determine the condition of the eggs, developing larvae, and the foodplants. Plants and larvae were misted with water each time they were examined. The laboratory in which the photochambers were kept was light-tight, and was totally darkened before the chambers themselves were opened. Under these conditions the "black-lights" emitted so little visible light that it was difficult to find the individual eggs and larvae in the experimental chambers.

Results

Results of the diapause induction experiments are shown in Table 1. The experimental "black-light" and control white light chambers gave comparable overall results. All surviving larvae on long-day underwent direct development whereas the majority of short-day larvae entered diapause. Only four short-day larvae showed direct development under "black-light". None of the short-day insects reared in white light developed directly. Mortality was minimal (11.5%) for the early larval instars and was evenly distributed among the groups.

Chi square analyses of the Table 1 data show no significant differences exist between the "black-light" and control regimes when comparing the numbers of larvae which died, developed directly, or those which diapaused. For short-day, a 2 × 3 contingency test yielded $\sum \times \frac{2}{2} = 4.43$, with p > 0.10. For long-day, a 2 × 2 analysis gave $\sum \times \frac{2}{1} = 0.31$, with p > 0.05. Thus, the null hypothesis that the larval responses are the same in both the experimental and control photoregimes is upheld in both cases.

All of the diapause termination experiments (Table 2) were carried out using long-day photoperiods. Resumption of larval activity following diapause is independent of photoperiod in *L. archippus*. Repeated observations by Platt (unpubl.) show that diapause termination can take place either in long-day or short-day photoperiods. Our present experiments show that diapause termination occurs equally well in

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[3]In a preliminary experiment to determine whether larvae would survive in the "black-light" photochambers, four eggs of the banded purple butterfly, *Limenitis arthemis* (Drury), from Vermont were placed on a willow plant in experimental ("black-light") conditions. One larva soon disappeared, and could not be found in the dim light. The other three grew well, underwent normal metamorphosis, and produced perfect adults. Both *L. arthemis* and *L. archippus* exhibit similar facultative diapause responses (Greenfield & Platt, 1974). The availability of strains was the sole criterion for choosing which species to use in the main experiments.
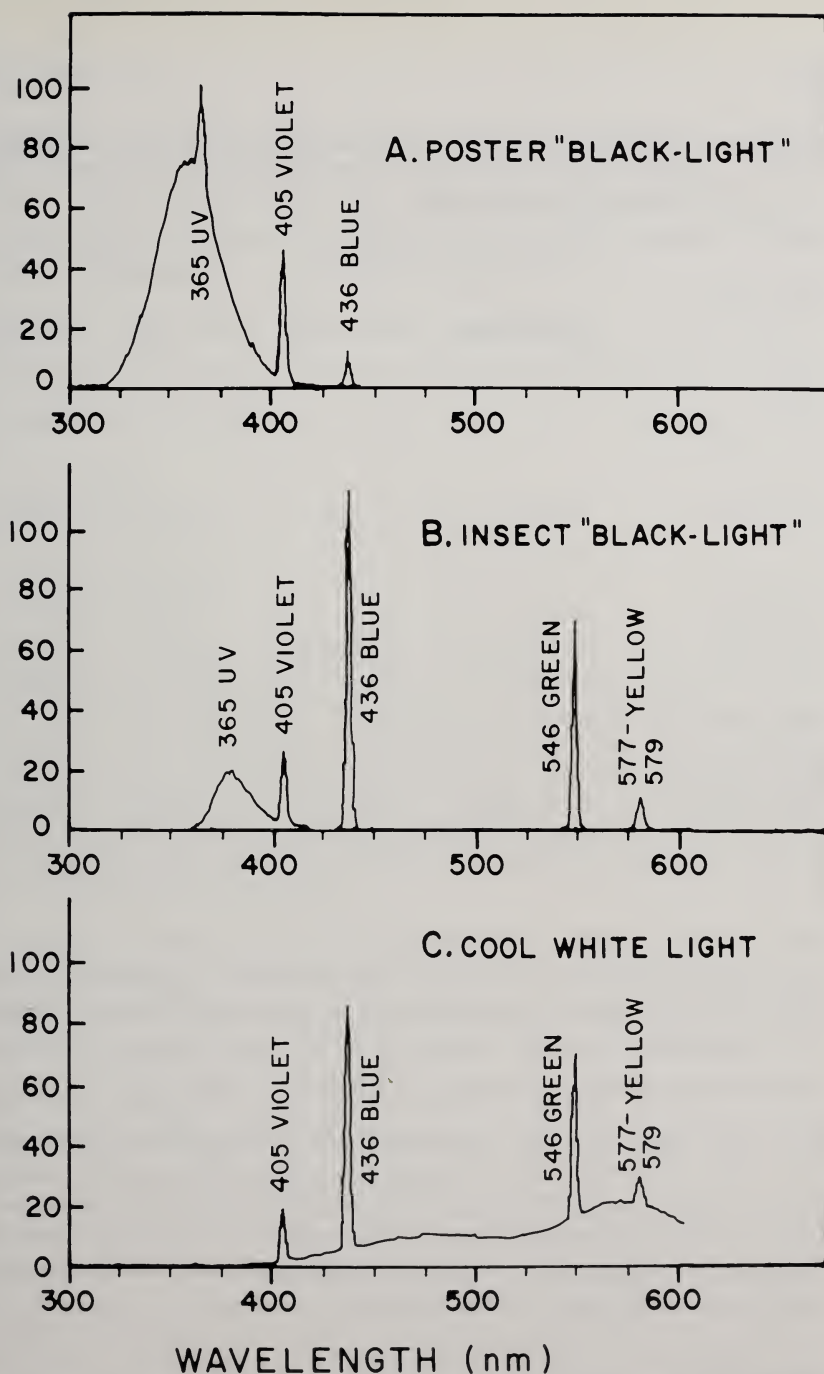
Fig. 1. Comparative emission spectra of G. E. flourescent bulbs (No. F15T8, 15 watt). The poster "black-light" (A) emits a partial spectrum with most wavelengths within the UV range (between 313-400 nm), and peaking at 365 nm. Additional visible lines occur at 405 nm and 436 nm, producing a dim, deep violet color. Both the insect "black-light" (B — shown for comparative purposes only), and the cool white tube (C) have additional emission peaks at 546 nm and between 577-579 nm as well. These spectra were measured for us by T. W. Cronin of UMBC using a microspectro-photometer as described in the methods section.

Table 1.   Diapause induction in Maryland *L. archippus* larvae sub-
             jected to "black-light" (experimental) and white light
             (control) photoperiods.

Photophase	Short-day (LD 8:16)		Long-day (LD 16:8)	
	"Black-light"	White light	"Black-light"	White light
Initial No. of eggs	21	20	10	10
No. & % dying	1 (4.7%)	2 (10%)	3 (30%)	1 (10%)
No. & % of survivors diapausing	16 (80%)	18 (100%)	0 (0%)	0 (0%)
No. & % of survivors showing direct development	4 (20%)	0 (0%)	7 (100%)	9 (100%)

both the "black-light" and white light chambers under long-day condi-
tions. Emerging larvae in both groups completed development success-
fully. All mortality encountered in these experiments was attributed to
larval parasitism, which was equal in both test groups. A 2 × 2 chi
square test of these data gave $\sum \times \frac{2}{1}$ (Yates) = 0.00, with p > 0.90. All of
the larvae used in these experiments had been wild-collected. Thus,
they had been exposed to ambient (outdoor) photophase until we
collected them in December and January prior to the experiments. The
larvae exhibited no apparent physiological or metabolic difficulties
adjusting to either the artificial photoregimes or other laboratory
conditions to which we subjected them.

Discussion

Insects in general, and Lepidoptera in particular possess visual
sensitivity which peaks in the UV range between 320-400 nm (Lutz,
1933; Goldsmith, 1961; Ferris, 1972; Goldsmith & Bernard, 1974;
Platt, et al, 1984). However, Lepidoptera and other insects can perceive
colors in the visible portion of the spectrum as well (Burkhardt, 1964;
Ichikawa & Tateda, 1982). Insect perception of infrared wavelengths

Table 2. Diapause termination in over-wintering *L. archippus* larvae
          collected in hibernacula near Conowingo Dam (Cecil Co.)
          MD. Larvae were reared under long-day (16L:8D) photo-
          period at room temperature with high moisture in the
          chambers.

	Black light	White light
No. of hibernacula with live larvae	10	10
No. & % dying (all parasitized)[1]	4 (40%)	3 (30%)
No. & % of survivors maturing to adults	6 (100%)	7 (100%)

[1]The braconid wasp parasite was *Apanteles limenitidis* Riley. Parasitized larvae
emerged from their hibernacula (terminated diapause) and fed briefly. Soon
they became inactive and never molted beyond third instar. Wasp maggots
emerged from the dying larvae and spun tiny yellow silk cocoons nearby. Each
larva yielded a single wasp. Adult wasps emerged about one week later. The
parasites obviously regulate their own cyclic development to correspond with
that of their host, since the larvae had been parasitized the previous autumn
prior to entering their hibernacula.

(600 nm and above) has not been well-documented in most species.
Often the individual ommatidia of insect compound eyes are specialized
for receiving a specific spectral range. Individual stemmata (important
larval photoreceptors) also are known to respond to specific wavelengths
in the same manner (Ichikawa & Tateda, 1982). However, these
stemmata (larval ocelli) are not believed to be functional in diapause
responses (Tanaka 1950, a, b, c, 1951, a, b).

Insects can respond to low intensities of light. Chapman (1969) states
that intensities above 1.0 foot-candle (f.c.) are sufficient to induce photo-
responses. Above this level, light intensity is not important in insect
photoreception. In both our experimental and control photochambers
the light intensities were well above these minimal levels. Earlier
studies on *L. archippus* larvae done in our laboratory revealed that
white light intensities as low as 0.10 f.c. were sufficient for inducing
either larval diapause or direct development, although adults from
larvae reared under such extreme conditions often possessed malformed
wings (Frankos & Platt, pers. obs; Platt, 1984).

Our experiments demonstrate that exposure to short-day "black-
light" photophase regimes induces facultative larval diapause in *L.
archippus*. Photoregimes consisting of the blue-violet and UV portions

of the spectrum will either induce and terminate diapause, or produce direct development, just as well as those consisting of white light do. Only four of 20 larvae in one short-day "black-light" group failed to diapause, but even here 80% of the larvae made hibernacula and entered diapause as did all under white light. The failure of all larvae to enter diapause is not unexpected for such a complicated life history trait which is under polygenic control (Hong & Platt, 1975; Williams & Platt, 1987). Failure to diapause occurs in natural populations of *Limenitis spp.* in the late summer and autumn. As the ambient photoperiod decreases, a few prediapause larvae continue to show direct development late in the season, when most others are diapausing (Weed, 1926; Greenfield & Platt, 1974). The "black-light" portion of the spectrum may not be the only portion to which these larvae respond. This portion may not even be necessary for diapause induction, but it is sufficient for eliciting the same responses that occur in white light. Clark & Platt (1969) suggested that the grey-white saddle patch of 2nd and 3rd stage *Limenitis* larvae may represent a photosensitive region. Future experiments are planned to investigate the possibility that the saddle patch is photosensitive, as well as a cryptic pattern.

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Suppression of the Black Phenotype in Females of the *P.glaucus* Group (Papilionidae)

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Abstract. Crosses between *Papilio g.glaucus* and *P.eurymedon* produced fertile offspring of both sexes, and backcrosses to *P.g.glaucus* revealed an autosomal suppressor in *P. eurymedon* which prevents expression of the black female phenotype of *P. g. glaucus*. Similar suppressors are demonstrated in *P. rutulus, P. multicaudatus* and *P. g. canadensis*.

Introduction

It is well known that in *Papilio glaucus* Linnaeus 1764, black females usually produce black daughters and yellow females yellow ones, irrespective of the provenance of the male. Occasional exceptions to this rule have been reported over many years and various explanations given (Clarke and Sheppard, 1959; Clarke et al., 1976). The present paper highlights the importance of autosomal genes which suppress, to a greater or less extent, the black female wing pattern. This can occur in the wild or be laboratory produced, and the phenomenon occurs in various species of the group.

In Section I we report a new example, bred by one of us (D.A.W.) in hybrids between black *glaucus* and *Papilio eurymedon* Lucas 1852.

Section II deals with further examples of suppression of black by *P. rutulus* Lucas 1852, *P. glaucus canadensis* Rothschild & Jordan 1906 and probably by *Papilio multicaudatus* Kirby 1884 (C.A.C.).

Section I: Suppression of Black in Hybrids Between *P. glaucus* and *P. eurymedon* (D.A.W.)

Papilio eurymedon (Fig. 1&2) is closely related to two other North American Swallowtails, *Papilio glaucus* (Fig. 11-13) and *Papilio rutulus* (Brower, 1959). Although laboratory crosses between *P. eurymedon* and *P. rutulus* have not been reported, Wagner (1978) described an almost certain male hybrid of these species from Idaho. In 1956 hybrids were

obtained between black and yellow female *glaucus* and male *P. euryme-don* (see Clarke and Sheppard, 1957) but only male insects were produced. In the present paper an account is given of female hybrids which were obtained (D.A.W.), and these are very informative as regards a gene suppressing the black of *glaucus*.

Materials and Methods

   P. eurymedon were provided by Michael Collins from the vicinity of Nevada City, Nevada Co., California and Monitor Pass, Mono Co., California. They were collected as pupae from native food plants, *Ceanothus integerrimus* Hooker & Arnott (Rhamnaceae) and *Prunus virginiana*, var. *demissa* (Nuttall) (Rosaceae), in late summer 1984 and 1985 and eclosed in the laboratory in Blacksburg the following springs. *P. glaucus* were reared from local stock (Montgomery Co., Virginia) or from Wisconsin and Illinois stock provided by J. Mark Scriber. The latter originated from south of the principal zone of interaction of *P. g. glaucus* and *P. g. canadensis* in Wisconsin (Scriber et al. 1986 and see Section II). The insects were hand-paired, and the females laid eggs on *Prunus serotina* Ehrhart (a local foodplant of *P. glaucus*). Larvae were reared on this species, either in tight plastic boxes or on leafy stems kept turgid in Aquapics® in ventilated plastic canisters. Rearing was on natural mid-summer day length supplemented to 15 to 16 h by artificial light.

   Samples of *P. glaucus* from Virginia and West Virginia and of *P. eurymedon* from northern California and western Oregon were used for morphological comparisons with the hybrids. *P. eurymedon* differs from *P. glaucus* most conspicuously in ground color, which is white or very pale yellow in the former but bright yellow in males and some yellow females of the latter. Some yellow females of *P. glaucus* are more orange-yellow. The black stripes and wing margins of *P. eurymedon* are broader than those of *P. glaucus*. As an index of the extent of the black pattern, the width of the under forewing black margin from its inner edge to the margin of the wing along vein Cu_1 was divided by the length of vein Cu_1 from the cell to the wing margin. The resulting ratio separates *P. glaucus* from *P. eurymedon*.

Results

   Table 1 summarizes the successful crosses and Table 2 the unsuccessful ones. The F_1 hybrids (Broods 85.1 and 86.1, Figs. 3, 4, 15) are nearly intermediate between the parental species in the black pattern, in the larval thoracic eye spots (as in Clarke and Sheppard, 1957, Fig. 1) and in pupal proportions. As Clarke and Sheppard (1957) noted, the hybrid pupae do not show the green/brown dimorphism of *P. eurymedon*, all being brown as in *P. glaucus*. In fact the female pupa of brood 85.2 had some green markings, but they were in areas in which occasional *P. glaucus* pupae are green and not in the well-defined zones in which that color is found in green *P. eurymedon* pupae. In both sexes the ground color of the wings is nearly as yellow as that of *P. glaucus*. The submarginal spots on the upper and under sides of the hindwing of *P.*

Table 1. Successful matings between *Papilio glaucus* and *P. eurymedon*.

Mating No. and date	Source of Parents Mother	Father	Eggs Laid	Eggs Devel.	Eggs Hatch.	Pupae	Eclosions
85.1 6 June 85	*eurymedon* (Nev. City, CA)	*glaucus* (WI)	17	15	15	5 ♂♂ 2 ? sex	2 ♂♂ 3 ♂♂ died as pupae 2 ? sex lost
85.2 6 June 85	yellow *glaucus* (WI)	*eurymedon* (Nev. City, CA)	28	3	3	1 ♀ 1 ? sex	♀ pupa died Nov 86 Other pupa lost
86.1 25 May 86	*eurymedon* (Monitor Pass, CA)	*glaucus* (unknown)	31	30	27	13 ♀♀ 13 ♂♂	13 yellow hybrid-like ♀♀ 13 hybrid-like ♂♂
85.3 3 Aug 85	black *glaucus* (WI x IL)	F₁ ex 85.1	66	22	21	10 ♀♀ 9 ♂♂	2 black ♀♀ both intermediate 2 yellow ♀♀ 3 ♂♂ 6 ♀♀, 6 ♂♂ died as pupae
86.7 15 July 86	yellow *glaucus* (unknown)	F₁ 'G' ex 86.1	46	44	36	5 ♀♀ 11 ♂♂	4 yellow ♀♀ 9 ♂♂ 1 ♀, 2 ♂ ♂ died as pupae
86.12 17 July 86	yellow *glaucus* (unknown)	F₁ 'L' ex 86.1	11	3	3	2 ♀♀	1 yellow ♀ 1 ♀ died as pupa
86.8 15 July 86	F₁ 'J' ex 86.1	F₁ 'H' ex 86.1	29	29	8	2 ♀♀	1 ♀ pupa alive, Mar. 88 1 ♀ died as pupa
86.9 16 July 86	yellow backcross ex 85.3	*glaucus* (unknown)	51	37	15	7 ♀♀ 7 ♂♂	1 yellow ♀, 6 black ♀♀ 5 ♂♂ 2 ♂ died as pupa
86.11 17 July 86	F₁ 'O' ex 86.1	F₁ 'Q' ex 86.1	15	15	3	2 ♂♂	2 ♂♂

Table 2.   Unsuccessful matings between *Papilio glaucus* and *P. eurymedon*.

Mating No. and date	Source of Parents Mother	Father	Remarks
86.3 28 May 86	yellow *glaucus* (unknown)	*eurymedon* (Nev. City, CA)	14 infertile eggs (no spermatophore)
86.4 31 May 86	*eurymedon* (Nev. City, CA)	*glaucus* (unknown)	41 infertile eggs
4 June 86	"	*glaucus* (unknown)	28 infertile eggs (1 tiny spermatophore)
86.5 14 July 86	yellow *glaucus* (unknown)	F_1 'A' *ex* 86.1	12 infertile eggs
19 July 86	"	F_1 'L' *ex* 86.1	unsuccessful pairing
19 July 86	"	F_1 'Q' *ex* 86.1	very long pairing (1 spermatophore?)
86.6 14 July 86	F_1 'B' *ex* 86.1	F_1 'D' *ex* 86.1	20 infertile eggs (1 spermatophore)
86.10 17 July 86	F_1 'N' *ex* 86.1	*glaucus* (unknown)	2 infertile eggs (very long pairing, no spermatophore)
86.13 29 July 86	F_1 'Y' *ex* 86.1	F_1 'P' *ex* 86.1	39 infertile eggs (1 spermatophore)
86.14 29 July 86	yellow *glaucus* (unknown)	F_1 'T' *ex* 86.1	23 infertile eggs (1 spermatophore)

glaucus are variable in size, shape and color but are usually rounder and oranger than those of *P. eurymedon*. The hybrids are also variable in these spots but are closer to *P. glaucus* in color and intermediate in size and shape. In all respects the male hybrids in broods 85.1 and 86.1 resemble those described by Clarke and Sheppard (1957) from the reciprocal species cross.

Brood 85-3, a backcross of a male F_1 from brood 85.1 to the black female form of *P. glaucus*, produced males (Fig. 5) and females of both forms: two black ones with a somewhat intermediate phenotype (Fig. 6), resembling occasional specimens taken in Virginia (Fig. 14), and two yellow ones (Fig. 7). One of the yellow females was backcrossed again, to a male *P. glaucus* (brood 86.9). All of the female pupae developed, and they produced six black and one yellow adults (Fig. 9 and 10; male in

Figs. 1–14. Species and hybrids of *Papilio*. 1. ♂ *eurymedon* (Nevada Co., California) Forewing base-to-tip = 52 mm, all other figures to the same scale; 2. ♀ *eurymedon* (Lake Co., Oregon); 3. F_1 ♂ (brood 86.1, ♀ *eurymedon* x ♂ *glaucus*); 4. F_1 ♀ (as in Fig. 3); 5. Backcross ♂ (brood 85.3, black ♀ *glaucus* x ♂ *ex* 85.1); 6. Backcross ♀ (as in Fig. 5); 7. Backcross ♀ (as in Fig. 5); 8. 2nd backcross ♂ (brood 86.9, yellow ♀ *ex* 85.3 x ♂ *glaucus*); 9. 2nd backcross ♀ (as in Fig. 8); 10. 2nd backcross ♀ (as in Fig. 8); 11. ♂ *glaucus* (Montgomery Co., Virginia); 12. ♀ *glaucus* (reared, Montgomery/Giles Co., Virginia); 13. ♀ *glaucus* (Montgomery Co., Virginia); 14. ♀ *glaucus* (Giles Co., Virginia, 1970).

Fig. 8). Fig. 15 shows that the variation in the forewing black margin ratio is inherited in hybrids and backcrosses as a quantitative trait with little evidence of dominance.

Discussion

Brood 86.1, and backcross and F_2 broods 86.7, 86.9, 86.11 and 86.12, show that the cross *eurymedon* ♀ x *glaucus* ♂ can be completely compatible, to the extent that fertile males and females are produced. All pupae of brood 86.1 eclosed 12-13 days after pupation, the normal minimum time for imaginal development. Taken with Clarke and Sheppard's results (1957) and brood 85.1, in all of which only male hybrids eclosed, brood 86.1 suggests that there is variation in the crossability of the two species and that Haldane's Rule need not apply (Haldane, 1922). Thus one of the reasons that Brower (1959) judged *P. glaucus* more closely related to *P. rutulus* than to *P. eurymedon* is sometimes removed. More crosses will be needed to assess the variation in cross-compatibility among these three species.

The ground color of yellow female *P. glaucus* is often just like that of males, and the genes responsible for it should therefore be autosomal (or X-linked), being found in both sexes. The black pigment, which Clarke and Clarke (1983) believe is "added" in black females, is of course Y-linked in its inheritance (Clarke and Sheppard, 1962; Clark and Clarke, 1983). The female hybrids in brood 86.1 support the view that yellow is autosomal or X-linked, because they are nearly as yellow as *P. glaucus* but are carrying a Y chromosome from *P. eurymedon* The blue scaling of *P. glaucus* females appears also to be autosomal (or X-linked) since, although *P. glaucus* males usually lack the blue, and *P. eurymedon* has reduced blue scaling, the female hybrids have nearly full expression as in *P. glaucus*. The male parent evidently carried the genes, but they were expressed only in females.

The two yellow daughters in 85.3 (Fig. 7) were a surprise, since all the daughters should be carrying the mother's Y chromosome, and there is ample evidence that black is Y-determined (Clarke and Sheppard, 1962). This suggests that *P. eurymedon* has a suppressor of that black phenotype, as discussed below in *P. g. canadensis* (Scriber et al., 1986) and *P. rutulus* (Clarke et al., 1976). The possibility of a suppressor was tested by a further back cross of one of the yellow daughters in brood 85.3 to a male *P. glaucus* (brood 86.9). Black reappeared in six of the seven female offspring (not different from a 1:1 ratio) and this could have been because the yellow female parent was heterozygous for the suppressor. The suppressor cannot be X-linked, because the mother in 86.9 passed it to her yellow daughters but would have passed an X only to her sons. It also cannot be Y-linked, because an F_1 male passed it to some of his daughters (brood 85.3). There are therefore good grounds for invoking an autosomal suppressor of black in *eurymedon*, though another remote
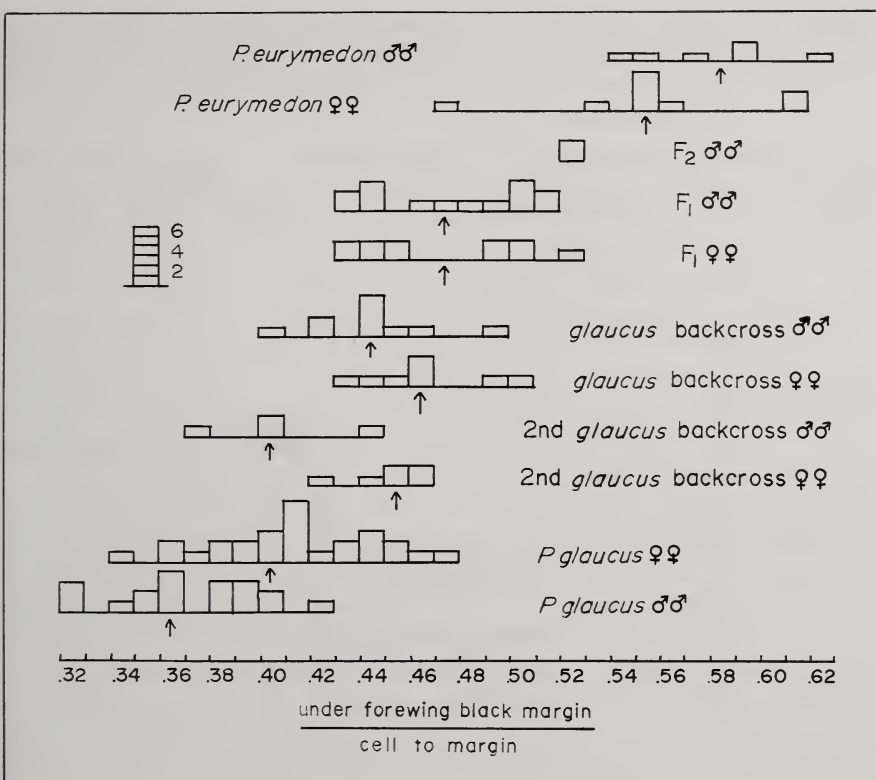
Fig. 15. Distributions of the relative width of the forewing black margin of *P. glaucus*, *P. eurymedon* and hybrids between them. Relative width is given as the ratio of black margin to the distance from cell to margin, measured along vein Cu_1. Means are marked by arrows.

possibility must be mentioned. The suppressor could have been introduced from *glaucus* of Wisconsin stock by the male parent of the original cross 85.1, but arguing against this are the facts that the Wisconsin male came from south of the range of *P. g. canadensis* and had a black mother and, more importantly, that among the black *glaucus* broods raised in Blacksburg from that particular stock there were none with suppression of the black phenotype.

Section II: Suppression of Black in Hybrids Between *P. g. glaucus* and *P. rutulus*, *P. g. canadensis*, and *P. multicaudatus* (C.A.C.)

There are hybrid zones where naturally occurring crosses can take place between some of these species (see map in Scriber et al. 1986) and all are easy to initiate using the hand-pairing technique.

Hybrids between *P. g. glaucus* and *P. rutulus* (Table 3)

In 1955 we hand-paired a female *rutulus* with a male *glaucus* and obtained 10 males and 8 yellow females (Clarke and Sheppard, 1955),

Table 3.   Crosses between black *glaucus* females and *rutulus* males
where suppression might occur. Some of the black insects had
yellow "brackets" on the forewings, but these are probably
normal variants.

Type of Cross	Brood No.	Parent		Offspring			
		Mother	Father	♂♂ ♀♀	Black ♀♀	Interm. ♀♀	Yellow ♀♀
F₁	14013	black glaucus	*rutulus* California	18	0	2[†]	0
"	15416	"	*rutulus* Vernon, B.C.	1	0	0	2
backcross	8455	"	glauc/rut F₁ hybrid	8	4	0	2
"	9608	"	"	13	6	0	1
"	9699	"	"	8	3	1	0
"	14173	"	"	18	3	4	0
2nd back.	14655	"	14173	25	16	2	0
"	9769	"	ex bl. glauc. ♀ x (glauc/rut) F₁♂	14	8	0	0
"	14639	"	"	16	4	0	0
"	14642	"	similar to 9769 and 14639	21	17*	1	0
3rd back.	14761	"	ex 14639	9	4	1	0
"	14763	"	"	17	21	0	0

* 6 with yellow showing through papery wings, 11 normal black.
[†] Ecdysterone treated.

and in the same year found a similar situation (unpublished) when the
mother was yellow *glaucus* and the male *rutulus*. However, importantly,
the F₁ cross between a black female *glaucus x rutulus* male, brood
14013, only yielded females when ecdysterone was injected into the
pupae. Then females intermediate in color (and resembling those in
brood 85.3, above) were produced. This suggested that here *rutulus*
carried a gene which partially suppressed the black pigment (Clarke et
al., 1976, Clarke and Willig, 1977, Clarke and Clarke, 1983). Later, in
our brood 15416, (previously unpublished) a black *glaucus* female
mated to a male *rutulus* from Vernon B.C., Canada, produced one male
and two *yellow* females, suppression of the black here being complete.
There was also evidence of suppression on back crossing some male
glaucus/rutulus F₁ hybrids to black *glaucus* females, since we occasion-
ally obtained broods where the female offspring segregated for black
and yellow wing color. On the whole, however, yellow was less evident
in the backcross (Table 3).

   More difficult to assess from the point of view of the suppressor are
minor degrees of yellow in black females. Sometimes the yellow shows
through and sometimes there are yellow "brackets" (see Clarke and
Clarke, 1983, Figs. 8 and 10). These might be due to partial suppression

or be normal variants of the form, particulary as there is some evidence that the black pigment is laid down late in development (Clarke and Willig, 1977).

Hybrids between *P. g. glaucus* and *P. g. canadensis* (Table 4−8)

The ranges of these two subspecies overlap, and *canadensis* also has common ground with *P. eurymedon* and *P. rutulus*. All these three butterflies are monomorphic, none having a black form, and it would not be surprising if black in *P. g. glaucus* were suppressed in the northernmost part of its range, where *canadensis* will have naturally hybridized with it. This is what in fact happens, but we are stating the case with hindsight, for it was Mark Scriber and his colleagues who greatly clarified the problem of the five species mentioned in this paper (personal communication 1983, Scriber et al., 1986).

Tables 4,5,6 and 7, taken from Scriber et al. (1986), give the details of families where these fundamental principles obtain. Table 4 shows that black is suppressed in F_1 hybrids between *P. g. glaucus* and *P. g. canadensis*. The suppressor is transmitted by F_1 males in backcrosses to black *glaucus* females, since both yellow and black daughters appear (Table 5), but not by "suppressed" yellow backcross females in crosses with *glaucus* males (Table 6). These results are consistent with Scriber el al.'s (1986) hypothesis that the suppressor is X-linked. We ourselves have two similar examples in Table 8. The first (brood 18288) derives from a black female *glaucus* mated to *canadensis*, and this produced yellow females (cf. Table 4); the second (brood 18344) was bred by using a yellow "suppressed" female 18288 mated to a Georgian male (well south of the *canadensis-glaucus* interface) and demonstrates the re-appearance of black (cf. Table 6).

Thus the matter at first sight seems simple - the suppressor is the result of a single autosomal or X-linked gene dominant in effect, and in the examples given there is clear-cut segregation black/yellow. But there are problems.

In Scriber's F_2 results (Table 7) half of the female offspring should be black, but no black appeared. Furthermore, in the backcross to black (see tables 3 and 8) the ratios are not strictly Mendelian, and in practice both in the field and in the laboratory clear-cut black/yellow are often blurred; all grades from black through intermediates to yellow are encountered. An attempt to explain the genetics of this is made in the general discussion; all we wish to emphasize here is that a suppressor mechanism undoubtedly exists in *P. g. canadensis*.

Hybrids between *P. g. glaucus* and *P. multicaudatus* (see Table 9)

In the F_1 broods using either black or yellow female *glaucus* and hand-mating them to male *multicaudatus* we only obtained male offspring (68 in one brood), but in backcrosses of *glaucus* females to hybrid males females were obtained in 8 broods and the sex ratio was

Table 4.   Offspring of crosses between black *P. g. glaucus* females and
           P. g. canadensis males (from Scriber et al., 1986).

Pairing Code	Males	Females Yellow	Females Black	Pupae still in diapause at time information was given
74	2	1	0	0
73	18	17	0	7
112	4	0	0	5
4	1	3	0	5
39	18	4	0	26
75	49	2	0	54
113	7	0	0	10

Table 5.   Offspring of crosses between black *P. g. glaucus* females and
           F_1 hybrid males, *P. g. canadensis* ♀ x *P. g. glaucus* ♂ (from
           Scriber et al., 1986).

Pairing Code	Male	Female Yellow	Black
6	8	1	3
14	7	5	4
15	40	11	20

Table 6.   Offspring of crosses between various *P. g. glaucus* males and
           yellow females from the backcross of F_1 (*glaucus* x *canadensis*)
           ♂ x black *glaucus* ♀ (from Scriber et al., 1986).

Pairing Code	Male	Females Yellow	Black
148	2	0	2
154	1	0	7
157	2	0	7
225	4	0	1
155	3	0	1

not significantly upset. Seven of these broods were to yellow *glaucus*
females and therefore not informative as regards suppression, but in the
single backcross to black which produced butterflies (brood 6329, table
9) the offspring were two males and two yellow females, one of them

Table 7.   Offspring of crosses between yellow F_1 females (cross 73, Table 4) and F_1 males (*ex* black *glaucus* ♀ x *canadensis* ♂) (from Scriber et al., 1986).

Pairing Code	Male	Females	
		Yellow	Black
272	29	28	0
288	19	12	0
279	11	6	0

Table 8.   Hybrids between *P. glaucus* and *P. g. canadensis* bred from Scriber stock by CAC in England.

Brood No.	Parents		Males	Offspring	
	Mother	Father		Black Females	Yellow Females
18288	Black Wisconsin	*canadensis*	3	0	3
18344	Yellow 18288	*glaucus* (Georgia)	8	8	0

Table 9.   Hybrids between *P. glaucus* and *P. multicaudatus* (CAC)

Brood No.	Parents		Males	Offspring	
	Mother	Father		Black Females	Yellow Females
6139	black *glaucus*	*multicaudatus*	68	0	0
6329	black *glaucus*	6139	2	0	2

described as "dark yellow." Unfortunately these insects are lost, but there is no reason to doubt the record, particularly in the light of later developments with *rutulus, eurymedon* and *canadensis*.

More work is obviously indicated and we have pupae of both species (June 1987).

General Discussion

The purpose of this paper has been to bring together the evidence showing that in four monomorphic yellow Tiger Swallowtails there are suppressors which can inhibit the expression of the black form of *Papilio glaucus*. In *P. eurymedon* the suppressor is clearly autosomal, since it can be transmitted from a father or a mother to a daughter, but the critical evidence is lacking for the other species. If the suppressor in *P. g. canadensis* were also autosomal, the expected frequency of "suppressed" yellow daughters in the F_2 broods of Scriber et al. (1986, Table 7) would be 3/4 (rather than 1/2, as from the hypothesis of X-linkage), but the lack of black daughters in those broods is still significant. In all other broods the expectations are the same for both modes of inheritance. Why these suppressors are present is not known. If *P. g. canadensis* and the three western species are derivatives of *P. glaucus* populations with female yellow/black dimorphism, then the suppressors may have been part of the genetic system that cut them off from the ancestral species. Otherwise the existence of suppressors in populations far from the nearest overlap with *P. g. glaucus* (e.g., *P. eurymedon* in central California) is difficult to explain. On the other hand, the history of speciation in the *glaucus* group, perhaps excepting *P. g. cnadensis*, is unknown.

Although it was thought possible (Clarke et al., 1976) to associate the presence of the nuclear heteropyknotic body only with the genetic factor for black, and therefore to be able to determine if the western "suppressed" species still carry that factor, it now appears that the heteropyknotic body is not a sure marker for black (Cross & Gill, 1979).

Suppression is common in Batesian mimetic butterflies, many species of which have mimetic patterns limited to females, although inheritance is autosomal. The mechanism of suppression of sex-limited traits is not known, but it appears to exist even in monomorphic species, since male hybrids do not show the mimetic patterns (Clarke and Sheppard, 1972). Crosses with non-mimetic species, however, usually produce more or less intermediate females, with little evidence of interspecific suppression (see *P. fuscus* x *P. polytes*, Clarke and Sheppard, 1972, Plate 42h).

The intermediate forms and unusual Mendelian ratios mentioned earlier would formerly have been explained by differences in expressivity of the gene or genes, but recent studies of the human X chromosome using the techniques of molecular biology suggest other possibilites. For example, an inherited form of mental deficiency appears to be transmitted as an X-linked recessive. The lesion responsible is an X chromosomal abnormality known as the fragile site, which can be induced in cell cultures by various procedures or chemicals. However, as with suppressors, problems soon arose. Occasional males with the fragile X were mentally normal, and some carrier females were affected. Pembrey

et al. (1985) erected a two-stage hypothesis by which the fragile X occurred as a mutant in the male X chromosome but produced no ill effect. However, at the formation of gametes in the daughter of such a male, recombination took place such that the fragile X mutation became more damaging, with half of the daughter's sons being handicapped and half her female offspring carriers. Of particular relevance to race crosses in butterflies are hybrid studies with the fragile X chromosome (Ledbetter et al., 1986). There the threshold for initiation of fragility by various chemicals (for example caffeine) is much reduced if the human X is isolated in a rodent genetic background. It seems not unlikely that everyone has a fragile-X site if the chromosome is suitably manipulated. Possibly the non-suppression of black pigment in *P. g. glaucus* is similarly the exceptional state in the *glaucus* group, with the other species carrying the potential for black permanently suppressed. That possibility could be tested with molecular techniques which have the potential of probing for suppressors in both humans and butterflies.

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New Species and new Nomenclature in the American Acronictinae
(Lepidoptera: Noctuidae)

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Abstract. Described as new species are *Acronicta sinescripta* from South Carolina, Louisiana, and Florida; *A. kendallorum* from Chihuahua, Mexico; *A. perblanda* from the region between North Carolina and Missouri southward to northern Florida and Louisiana; and *Cryphia cyanympha* from South Carolina, northern Florida, and eastern Texas. *C. cyanympha* is the only member of the tribe Bryophilini definitely known from eastern North America. *A. kendallorum* was reared from larvae on *Froelichia arizonica* (Amaranthaceae); *A. perblanda* is associated with cypress swamps, although it has not been reared; and *C. cyanympha* is related to a Caribbean group believed to feed on lichens of the genus *Usnea*. The host of *A. sinescripta* is unknown. *A. perblanda* is divergent and only doubtfully referred to the genus *Acronicta*. *Agriopodes jucundella* Dyar and *Bryolymnia huastea* Schaus from Puerto Rico, which appear closely related to *C. cyanympha*, are transferred to the genus *Cryphia* Hübner and considered synonyms, with *jucundella* being the older name. *Agriopodes teratophora* (Herrich-Schäffer) is transferred to the genus *Anterastria* Sugi in the Acontiinae.

Introduction

The three species from the southeastern United States treated in this paper have been known and recognized as undescribed for nearly 20 years, and questions concerning their identity have arisen repeatedly. It is time that they were named. I include also a new species of *Acronicta* from northern Mexico that might eventually be found to occur in the border region of the United States. Three of the new species are in the tribe Acronictini and placed in the genus *Acronicta* Ochsenheimer, although one of them is referred to this genus somewhat doubtfully, as I explain later. The fourth, a species of *Cryphia* Hübner, belongs to the tribe Bryophilini as currently understood. This moth, *Cryphia cyanympha*, n. sp., is particularly interesting because it is the only bryophiline definitely known to be present in eastern North America, belongs to a small group otherwise known only from the Greater Antilles, and is almost certainly a lichen feeder. Although *Cerma galva* Strecker, 1898 (=*Cryphia galva*, Franclemont and Todd, *in* Hodges, et al., 1983), was described from Clyde, Wayne County, New York, its type

has since been identified as a specimen of the western *Cryphia olivacea* (Smith, 1891) (R. W. Poole, pers. comm.), a species not otherwise known from the eastern United States. Strecker evidently cited a false type locality.

My assignment of *cyanympha* to the genus *Cryphia* followed a review of the species formerly listed under *Agriopodes* Hampson in North American lists, as well as a cursory investigation of *Bryolymnia* Hampson, and of species formerly referred to *Bryophila* Treitschke. It is in agreement with the arrangement of Franclemont and Todd (*in* Hodges et al. 1983: 136), in which species thought to be related to *Agriopodes fallax* (Herrich-Schäffer), the type species of *Agriopodes* (Figs. 31, 32), were left in that genus, and the remainder were combined with species transferred from *Cerma* Hübner to form the American section of the genus *Cryphia* (formerly *Bryophila* in much of the Old World literature) (Acronictinae: Bryophilini). This has nothing to do with the *Cryphia* of previous North American literature, in which the name was misplaced in the Acontiinae as a result of a misunderstanding of the type species. Those moths are now in the genus *Hyperstrotia* Hampson. The type species of *Cryphia* is the European *C. deceptricula* (Hübner). It is still uncertain whether *C. cyanympha* and its Caribbean relatives should be regarded as congeneric with any other species assigned to the Bryophilini, but within the present classification *Cryphia* is where they fit best. A thorough revaluation of *Cryphia, Bryophila, Bryoleuca* Hampson, and other related Old World genera and their type species is needed but beyond the scope of the present paper.

It seems clear that the North American species long known as *Agriopodes teratophora* (Herrich-Schäffer) (=*Bryophila teratophora* Herrich-Schäffer, [1854]) is misplaced and belongs in the genus *Anterastria* Sugi, 1982. This generic name was proposed for a closely related Japanese counterpart of *teratophora* originally described as *Erastria atrata* Butler, 1881 (Sugi, *in* Inoue et al., 1982, vol. 1:818; vol. 2:383, pl. 197, fig. 57). The American species therefore becomes *Anterastria teratophora* (Herrich-Schäffer, 1854), NEW COMBINATION, and it should be transferred to the Acontiinae, tribe Eustrotiini, following Sugi's arrangement. That would place it somewhere near *Lithacodia* Hübner in the North American fauna. However, the male genitalia of both species of *Anterastria* are disconcertingly similar to those of species of *Cryphia* treated in this paper, so much so that one might even be led to consider them congeneric on that basis. If the reassignment of *Anterastria* to the Acontiinae is correct, the resemblance to *Cryphia* must be a result of convergence. *Anterastria teratophora* was illustrated most recently by Covell (1984: pl. 25, fig. 19).

Acronicta sinescripta Ferguson, new species

Diagnosis. This is a southeastern species that most closely resembles *Acronicta oblinita* (J. E. Smith), especially the evenly gray, almost unmarked form *insolita*

Grote; but it differs in the configuration of dark markings associated with the reniform spot, the regular rather than dentate postmedial line (if visible), the grayer hindwings (white in both sexes of *oblinita*), and the absence of dark terminal dots along the outer margin of the hindwing. Also, on the underside, the forewing is much darker than the hindwing in *sinescripta*, almost as pale in *oblinita*, and both wings beneath lack the discal spot present in *oblinita*. Another species with which *sinescripta* could be confused is *A. lanceolaria* Grote, which does have traces of similar dark markings associated with the reniform. However, *lanceolaria* is larger, has a more produced and pointed apex on the forewing, lacks the basal streak and other dark forewing markings of *sinescripta*, often has a fairly prominent, sinuous, pale postmedial line, especially in females and, like *oblinita*, an almost white hindwing. *A. sinescripta* may be distinguished from *A. arioch* Strecker, which looks like a large, pale form of *oblinita*, by essentially the same differences that separate it from the latter species.

Further description. About same size and shape as *A. oblinita*. Male antenna laminate, finely setose, whitish-scaled dorsally, tapering to an almost simple tip; female antenna filiform, finely ciliate ventrally, weakly whitish-scaled dorsally; palpus slender, about as long as distance across front diagonally in both sexes, white ventrally, grayish or mixed black and white apically, black dorsally beneath eye; front narrower than eye in male, about as wide as eye in female, almost flat, with mixture of white and dark-gray or blackish scales; eye bordered posteriorly by a few dark scales but without heavy black border; vestiture of body light gray; head and thorax lightly streaked with darker scales and appearing slightly darker than abdomen; tegula and patagia similarly gray, unmarked; legs normal, stoutish, gray, unmarked; hindtibia somewhat swollen. *A. sinescripta, oblinita*, and others of this group lack the dark facial band comprised of black contiguous areas of front, palpi, tegulae, and eyes that create the black-masked appearance of most *Acronicta* species.

Wings elongated like those of *oblinita*, but forewing a little less pointed, its shape intermediate between those of *oblinita* and *lithospila* Grote. Upperside of forewing uniformly bluish gray, resulting from even mixture of whitish and gray scales; almost unmarked, although variable vestiges of pattern are present, as follows: thin, black, basal dash on cubital stem running about 6 mm toward middle of wing; thin, weak, black longitudinal streak running through outer end of cell, appearing to pass through and be interrupted by reniform spot, although reniform not really visible; this streak, usually dividing to form vaguely defined, longitudinal cell at that point, then continues as a faint, dark line on M_2 toward outer margin; other short, faint, black dashes may occur in outer third of forewing on R_4, M_1, and Cu_2. Some specimens show traces of a postmedial line that is evenly curved, subparallel to and quite near outer margin; others show a wide, very diffuse, dark transverse band through postmedial area of forewing or both wings. Hindwing whitish, variably dusted with gray scales, especially toward apex and costa. Fringes concolorous with wings or slightly paler. Underside of forewing gray, darkest mesially, usually paler near costa and in outer third. Underside of hindwing about like upperside, darkest toward costa. Length of forewing: holotype, 19 mm; other ♂♂, 18-19 mm. Allotype, 20 mm; other ♀♀, 19-21 mm.

Male genitalia (Figs. 16, 17). Valve broad, rounded, simple, with clasper consisting mainly of one large, stout process that does not quite reach costa;

uncus normal but delicate; juxta partly spinulate; vesica with cluster of about 14 medium-sized cornuti with fine, attenuated points.

Female genitalia (Fig. 29). These were compared with genitalia of *oblinita* and *lepusculina* Guenée, representatives of two groups to which I thought *sinescripta* might be related. It differs obviously from *oblinita* in having more elongated, pear-shaped bursa copulatrix, nearly twice as long as that of *oblinita*; longer, much more swollen, sclerotized and rugose ductus bursae; and more abruptly and deeply cleft posterior margin on eighth sternite. Ductus bursae adjoins corpus bursae apically, and entire bursa copulatrix and eighth sternite are of different form, the corpus bursae long and slender posteriorly, ending in zone of heavy sclerotization where it meets the very short ductus bursae, and the eighth sternite unnotched but with wide, shallow concavity on posterior margin. On basis of female genitalia, *sinescripta* would appear more closely related to *oblinita* than to *lepusculina*.

Types. Holotype ♂, 4.2 mi. NE of Abita Springs, St. Tammany Parish, Louisiana, 8 April 1984, V. A. Brou (Fig. 1). Allotype ♀, same locality and collector, 16 June 1984 (Fig. 2). Paratypes: 1 ♀, same locality and collector, 20 August 1982; 10 ♂♂, same locality and collector, 17, 30 April, 7 May, 11, 15, 30 June, 3, 7, 8, 20 July 1983; 1 ♀, same locality and collector, 16 July 1983; 18 ♂♂, same locality and collector, 3 March, 1, 3, 4, 7, 11, 21 April, 4, 5, 14, 15, 18, 23, 26 June, 1, 21 (2), 28 August 1984; 1 ♀, same locality and collector, 21 June 1984; 1 ♀, MTF [Mississippi Test Facility, Natl. Air and Space Admin.], Hancock Co., Mississippi, 2 July 1973, R. Kergosien; 1 ♀, Gainesville, Florida, 30 March 1929; 4 ♂♂, Archbold Biological Station, Lake Placid, Highlands Co., Florida, 29 March 1959 (♂ genitalia slide 6751, J. G. Franclemont—Figs. 16, 17), 30, 31 March, 2 April 1959, J. G. Franclemont; 1 ♀, some locality and collector, 3 April 1959; 1 ♀, The Wedge Plantation, McClellanville, South Carolina, 20 August 1968, D. C. Ferguson (Fig. 3); 3 ♀♀, same locality, 23 May, 23 June, 7 August 1971, R. B. Dominick and C. R. Edwards. All as far as known were collected at light. Holotype and allotype in U.S. National Museum of Natural History; paratypes in National Museum, Canadian National Collection, Florida State Collection at Gainesville, British Museum (Natural History), and collections of V. A. Brou, J. G. Franclemont, and Bryant Mather.

Distribution. Coastal South Carolina to Highlands County, Florida, and westward through the Gulf States to Louisiana.

Early Stages. Unknown.

Remarks. I have known of this species since I collected a specimen in 1968, and shortly afterward found a second specimen, from Gainesville, in the collection of the U. S. National Museum. Several others were soon sent by other collectors, but all were females. When I prepared an earlier draft of this paper in the 1970's and sent it to Dr. Franclemont for his comments, I learned that he had collected four males and a female in Florida in 1959. He kindly responded by sending the slide from which my illustration of the male genitalia (Figs. 16, 17) was then prepared. Then in 1982, 1983, and 1984, Vernon A. Brou, at one locality in Louisiana, collected three times as many specimens as were previously known, and these include such fresh, bright examples that I chose two of them as holotype and allotype.

Acronicta kendallorum Ferguson, **new species**

Diagnosis. A gray-dusted, medium-sized *Acronicta* of rather nondescript appearance, perhaps most resembling a dark *A. sperata* Grote or *rubricoma*

Guenée, with similar wing shape and pattern but differing from these and apparently from all other North American species of the genus in having pectinate male antennae and very short, hairy palpi in both sexes. Male genitalia normal for the group and similar to those of *A. impressa* Walker, although armature of valve differently oriented, juxta differently shaped, and vesica with more and longer cornuti. Known only from a small reared lot from southwestern Chihuahua, Mexico.

Further description. Male antenna bipectinate with branches so short and closely set as to appear laminate, each lamellum about as long as thickness of shaft and orange brown; shaft scaled dorsally with black and white scales; female antenna simple; palpus of both sexes not or only slightly protruding beyond front, clothed in hairlike scales; front slightly protuberant; eye of male about average for genus, about as wide as front, that of female three-fourths as wide as front; tongue moderately developed, not large; ocellus present, small; legs heavily clothed with long scales, all spurs present; epiphysis large but not quite reaching end of foretibia.

Thorax and abdomen gray, resulting from mixture of dark-gray and white scales; front and vertex gray, with thin white margin adjacent to eye; dark mask that passes from palpi back through eye in many *Acronicta* species only vaguely apparent, not contrasting; legs gray, tarsi dark with white ring marking end of each segment.

Upperside of forewing with an almost equal mixture of white and blackish scales and with usual pattern of antemedial and postmedial bands and orbicular and reniform spots present but not very distinct; dark scales in these elements of pattern seen to be symmetrically aligned in transverse rows under magnification; costa with about eight small black spots that indicate otherwise largely obsolescent transverse lines or bands of forewing pattern; black and white checkered fringe preceded by weak, discontinuous, dark terminal line. Hindwing pale gray, nearly white, with slight dusting of darker gray-brown scales toward outer margin, especially along veins; a weak, dark terminal line; and white, unmarked fringes. Underside of wings almost unmarked; forewing light grayish with very diffuse, gray reniform; hindwing nearly white. Length of forewing: holotype ♂, 15 mm; other ♂♂, 14, 15 mm; allotype ♀, 16 mm.

Male genitalia. As illustrated (Figs. 20, 21).

Female genitalia. Not dissected.

Types. Holotype ♂, Creel, ca. 2134 m (7000 ft.), Chihuahua, Mexico, reared 10 April 1979 from larva on "? *Froelichia arizonica* Thornber" (Amaranthaceae), Roy O. and C. A. Kendall (Fig. 4). Allotype ♀, same data but emerged 30 May 1979 (Fig. 6). Paratypes: 2 ♂♂, same data but emerged 7 May and 27 June 1979; 2 last-instar larvae in alcohol, same data but preserved 21 Sept. 1978. Holotype, allotype, and paratype larvae deposited in collection of U.S. National Museum of Natural History; paratypes returned to R. O. Kendall.

The exact type locality is about halfway up a small hill adjacent to the Motel Parador de La Montana. Creel is about 177 km (110 mi.) southwest of the city of Chihuahua in the region of the Sierra Tarahumara, and north of Copper Canyon and Urique Canyon.

Distribution. Known only from the type locality.

Early stages. Type material was reared from larvae collected from a plant tentatively identified by R. O. Kendall as *Froelichia arizonica* Thornber (Amaranthaceae). Many larvae were present, some of them feeding on another, still unidentified plant that had long, succulent stems and peltate leaves. Only a

few were kept for rearing because an acceptable substitute food could not be found. Twenty-five larvae were preserved (R. O. Kendall, pers. comm., 1985). Larvae that matured and pupated in late September produced adults the next spring, following a pupal diapause.

The larva (Fig. 15) is of a type that seems to place it in that section of the genus that includes *impressa* Walker and *perdita, noctivaga*, and *sperata* of Grote, but is conspicuously adorned with large, pale verrucae, contrasting boldly with the very dark integument. It also has a wide but segmentally interrupted and somewhat sinuous, lateral (subspiracular) band. The pale markings may have been white or yellow in life. The head and thoracic legs are nearly black, and the dark-brown body integument has a finely granulate texture. The verrucae bear numerous long, whitish, barbed hairs, and centrally, from the dorsal verrucae especially, arise one to four erect, blackish, barbed spines, almost as long as the whitish hairs. Length of two larval paratypes: 33, 47 mm.

Remarks. I am pleased to name this species for its collectors, Roy O. and Connie A. Kendall, through whose efforts not only the adult but also the larva and food plant have been made known to us.

Acronicta perblanda Ferguson, **new species**

Diagnosis. This is a small, delicate, light-gray species easily recognized by the straight black streak that runs often without interruption from the base to near the tornus of the forewing. The genitalia are distinctive, and there is a question as to whether it is a true *Acronicta*; but the pattern, including the black markings of the head and legs, are typical of the *lobeliae-laetifica-interrupta* group. *A. perblanda* would look very much like a diminutive *lobeliae* were it not for the absence of the black dash associated with the reniform spot and the exaggerated length of the basal and tornal dashes that may unite them as one continuous streak. The species is southeastern and rare in collections. Circumstantial evidence from collecting sites suggests an association with bald cypress or with some plant that grows in cypress swamps.

Further description. Antenna filiform, minutely ciliate beneath, that of male about as stout as longest tarsal segment, that of female much more slender than longest tarsal segment, both with mixture of white and gray scales dorsally; palpi of both sexes quite long, exceeding front by one-third their length, black with whitish scales ventrally on proximal half, at tip, and a few on inner surfaces; distal palpal segment small but visible; front somewhat protuberant, clothed in white scales with a few gray ones mixed in, except that scales of lower lateral corners, near palpus, are black; black areas of palpus, front, and tegula, together with eye, forming a unified band that creates a masked effect in usual manner of many *Acronicta* species; thorax and abdomen gray, clothed with mixture of gray and whitish scales; tegula margined laterally with black scales; short, black, middorsal streak just behind head, between patagia; scales on top of head, between and behind bases of antennae, white; broad border of black scales adjacent to eyes posteriorly; legs whitish with mixture of gray scales, except mid- and hindtibiae, which are marked with a very distinctive, heavy, full-length black streak on outer side; inner (dorsal) tibial spur of each pair at least twice as long as outer one.

Forewing somewhat elongated, about same shape as that of *A. lobeliae* but much smaller; ground color of upperside pale gray, resulting from mixture of white and light gray-brown scales, all markings black; most conspicuous

marking is long streak from base to point on outer margin just anterior to tornus; basal and tornal (anal) black dashes characteristic of such species as *lobeliae* and *interrupta* are longer in *perblanda*, being thinly joined across median space or nearly so, thus forming what usually appears as a continuous streak; smaller black dash in space between Cu_2 and 2nd A, immediately behind constricted or interrupted mid-zone of long streak, although this may be obsolescent; a few black scales along inner margin posterior to lesser dash; basal, antemedial, and what is probably postmedial line clearly outlined with black scales toward costa; basal line short, curved, much as in *A. interrupta*; antemedial and postmedial lines, if apparent, sharply inclined outwardly from costa, then acutely angled back toward base at radius, thus forming long dentations at those points; antemedial continuing posteriorly to form rounded lobe inwardly and lesser, blunted tooth outwardly before reaching large longitudinal streak; short dashes usually present at outer margin in folds between M_1 and M_2, and Cu_1 and Cu_2, and shorter ones in spaces between other veins, giving fringes a checkered appearance; dark discal spots hardly apparent. Black scales that form markings of forewing overlapped and offset, not arranged in straight rows that give ridged or striated effect characteristic of other species of *Acronicta* with similar markings. Hindwing dull grayish brown with whitish, faintly checkered fringes. Underside of forewing brownish, of hindwing light gray, with faint, very diffuse postmedial bands; hindwing with diffuse discal spot. Length of forewing: holotype ♀, 12.0 mm; other ♀♀, 13.0 mm; allotype ♂, 11.0 mm; other ♂♂, 10.5-12.0 mm.

Male genitalia. As shown (Figs. 18, 19). Everted vesica may be seen to have 10 long, very slender cornuti and numerous short ones.

Female genitalia. As shown (Fig. 30). Ductus bursae as long as corpus bursae, nearly cylindrical, somewhat rugose, sclerotized, rigid.

Types. Holotype ♀, McClellanville, South Carolina [Wedge Plantation], 20 April 1970, R. B. Dominick and Charles R. Edwards; USNM Genitalia Slide No. 52,174 (Fig. 7). Allotype ♂, same locality and collectors, 25 April 1973 (Fig. 8). Paratypes: 1 ♂, Hilliard [Nassau County], Florida, "4-2-46," F. H. Chermock; 1 ♂, Gainesville, Florida, 13 April 1963, blacklight trap, H. A. Denmark; 1 ♂, Jct. State Highway 101 and 181, Cartaret County, North Carolina, 30 April 1974, J. Bolling Sullivan (Fig. 9); 1 ♂, Edgard, St. John Parish, Louisiana, 13 April 1979, V. A. Brou; 1 ♀, same locality and collector, 30 March 1982; 2 ♂♂, 4.2 mi. NE of Abita Springs, St. Tammany Parish, Louisiana, 24 April 1983, 22 April 1984, V. A. Brou; 1 ♀, same locality and collector, 7 April 1984; 1 ♂, cypress-tupelo swamp with associated southeastern flora, Otter Slough Wildlife Area, Stoddard Co., Missouri, 28 May 1983, at blacklight, J. R. Heitzman (Fig. 10).

The holotype and allotype, which are deposited in the U.S. National Museum of Natural History, were taken in a light trap at the edge of the Santee Delta, on the south bank of the Santee River. Paratypes are in the Canadian National Collection, the Florida State Collection of Arthropods at Gainesville, and in the collections of V. A. Brou, Abita Springs, Louisiana, J. R. Heitzman, Independence, Missouri, and J. B. Sullivan, Beaufort, North Carolina.

Distribution. In cypress swamp areas from Cartaret County, just south of Cape Hatteras, North Carolina, and Stoddard County, Missouri, to northern Florida and southern Louisiana.

Early stages. Unknown. However, the occurrence of adults almost entirely in April (one taken in Louisiana on 30 March and one in Missouri on 28 May) indicates that the species is univoltine and probably overwinters as a pupa. The

localities all appear to have been in the vicinity of bald cypress, *Taxodium distichum* (L.) Rich.

Remarks. The female and to a lesser degree the male genitalia show such obvious similarities to those of *Acronicta ybasis* Dyar (1918: 345), a Mexican species, that the relationship must be close. Both have the wide, sclerotized, regularly cylindrical ductus bursae. The size, wing shape, and slender build are also similar, but the forewing pattern is different, *ybasis* having a distinct reniform and orbicular, and short basal and anal dashes only.

The correct taxonomic disposition of this species is not likely to be made without much more comprehensive revisionary study. But meanwhile, for purposes of collection arrangement, I would simply add it to the end of the list of North American *Acronicta* species, inasmuch as there seems to be nothing closely comparable except the Mexican *A. ybasis*.

J. G. Franclement suggested to me that the moth listed from Florida as a *Catabena* species by Kimball (1965: 104) is probably the same as *A. perblanda*. The specimens were supposed to be in the Los Angeles County Museum of Natural History but cannot now be found.

Cryphia cyanympha Ferguson, new species

Diagnosis. This is a small, green, recently discovered noctuid known from South Carolina, northern Florida, and eastern Texas. Its predominantly blue-green forewing might lead to confusion with *Cyathissa percara* (Morrison), an unrelated species of similar size and coloring that also occurs in the Southeast; but on closer inspection it is easily seen that the forewing pattern is different. The pattern and male genitalia are characteristic, and the illustrations should make identification simple. This moth belongs to a group of three or four closely related species that occur on islands of the Caribbean, at least on Cuba, Hispaniola and Puerto Rico, and of which only one seems to have been described (see remarks). The closest known species in the continental United States may be the southwestern *Cryphia viridata* (Harvey) (Figs. 23, 24).

Further description. Male antenna heavily ciliate, with setae about as long as width of shaft; female antenna slender, with short setae; shaft in both sexes with alternating transverse bands of light and dark scales dorsally. Head, scape, and thorax with light-green to whitish scales, patagia black tipped; front smooth, almost square; palpi of both sexes fairly long, nearly reaching top of front, blackish with third segment white; ocelli very small, inconspicuous; tongue moderately but not highly developed. Legs fairly short, rough-scaled, with long spurs, irregularly blotched and banded with dark-brown and whitish scales. Abdomen light gray brown, concolorous with upperside of hindwings, with admixture of black scales beneath.

Upperside of forewing light bluish green with black and white markings as follows: basal line black, prominent between costa and radius, otherwise obsolete except for triangular projection on cubitus and a few black scales near inner margin; antemedial and postmedial bands black, bordered with white, the former white on inner side, the latter on outer side; inner white border one or two scales wide, outer white border two or three scales wide; antemedial band evenly excurved, reflexed outwardly at 2nd anal; black part of antemedial band widening greatly at costa, less so at inner margin, with a broad rectangular

process extending outwardly as a black bar to end of cell, which is two-thirds distance to postmedial band, this being followed posteriorly by some black scales forming a second, less definite, rectangular configuration adjacent to the other but less than half its length; postmedial line missing near costa, thence sinuous, excurved at M_1 and at 2nd A, incurved about M_3, inclined outwardly and somewhat expanded at inner margin where its black scales closely approach those of antemedial band; black triangular spot at costa opposite end of discal bar, this probably being remnant of medial band otherwise wanting in this species; postmedial third of forewing with scattered black scales, especially in middle area near outer margin and near costa, probably representing fragmentary submarginal band; black scales at outer margin form a weak terminal line, preceded by border of white scales; fringes rather long, comprised of black-tipped gray scales, with vague greenish rays opposite ends of R_5, M_2, and M_3; costa margined with a few black scales between basal and antemedial bands, and with three small black patches in distal third, the first being opposite postmedial band and probably marking point at which it meets costa. Hindwing grayish brown, unmarked, thinly scaled, becoming slightly paler basally, and with proximal tier of fringe scales concolorous, outer tier whitish. Underside of forewing grayish brown, almost unmarked; basal two-thirds of costa dark, outer third with three dark spots separated by areas of whitish scales; outer margin with dark terminal line and moderately large, subcircular, light-greenish spot at apex; discal spot faint. Underside of hindwing an even mosaic of white and blackish-brown scales, except that there are fewer dark scales in space between cubitus and third anal vein; outer margin with dark terminal line, somewhat interrupted at vein endings and fading out toward inner angle. Length of forewing: holotype, 8 mm; other ♂♂, 7-8 mm; ♀♀, 7-8 mm.

Male genitalia. As figured (Figs. 27, 28). Similar to those of *Cryphia viridata* (Figs. 23, 24) but with simpler clasper, no transtilla, various differences in shape of other components, and very large cornutus on vesica, plus a closely set, seemingly deciduous clump of much smaller cornuti. Although moth looks more like *jucundella*, it seems no closer in genital characters to that species (Figs. 25, 26) than to *viridata*.

Female genitalia. Of a generalized type that could be acronictine or almost anything, but with good species characters. Although genitalia of female holotype of *C. huastea* Schaus were badly mutilated by whoever dissected them, making comparison of *cyanympha* with that species difficult, it appears that *cyanympha* has a funnel-like ostium only about half as large, a heavily sclerotized elbow in the ductus bursae lacking in *huastea*, a corpus bursae without numerous spicules that may be seen in *huastea*, and two very delicate signa, which together would equal no more than half the size of the one invaginated, cuplike, spiculate signum of *huastea*. Bursa of *huastea* either bilobate or distorted in such a way as to appear so. Bursa of *cyanympha* entire. Female genitalia of *C. viridata* also have funnel-shaped ostium but of different shape; otherwise simple, offering little basis for comparison, having simple, membranous, slightly elongated bursa copulatrix without either spicules or signa; ductus bursae shaped much like that of *cyanympha* but entirely membranous.

Types. Holotype ♂, University of Florida Preserve, Welaka, Putnam County, Florida, 24 March 1987, D. C. Ferguson (Fig. 12). Paratypes: 67 ♂♂, same locality and collector, 24, 25, 28 March 1987; 16 ♂♂, same locality, site 4, live

oak xeric hammock, 9-10 June 1986, J. B. Heppner and J. Powell; 89 ♂♂, same locality, some labelled Site 4 as above, others Site 5, slash pine-palmetto flatwoods, 17-21 March 1986, J. B. Heppner; 1 ♂, Gainesville, Alachua Co., Florida, 3 Oct. 1983, E. C. Knudson; 2 ♀♀, Withlacoochee State Forest, vic. Kirk Hill, Hernando Co., Florida, 6 Sept. 1986, L. C. Dow; 1 ♀, Rock Spgs., Kelly Park, 6 mi. N. of Apopka, Orange Co., Florida, 18 Feb. 1984, L. C. Dow; 1 ♂, McClellanville [Wedge Plantation], South Carolina, 12 May 1970, R. B. Dominick and C. R. Edwards; 1 ♀ (Fig. 11), same locality and collectors, 26 Apr. 1970 (Fig. 11); 2 ♂♂, New Waverly, Texas, 14 June 1964. A. & M. E. Blanchard; 2 ♂♂, Town Bluff (Dam B), Tyler Co., Texas, 15 Sept. 1975. Holotype and many paratypes in U.S. National Museum; others in Florida State Collection, Gainesville, and in the collections of E. C. Knudson, H. D. Baggett, and L. C. Dow. Paratypes will be distributed to other collections.

Distribution. Charleston Co., South Carolina; Alachua, Putnam, Orange, and Hernando counties, Florida; Tyler Co., Texas.

Early stages. Unknown, but the closely related *C. jucundella* (Dyar) from Puerto Rico is evidently a lichen feeder. In the original description Dyar (1922: 11) wrote: "Mr. Wolcott states that the larvae fed on lichens, being of the same color as the lichen, marked with brown, a beautiful example of protective resemblance." The type of *jucundella* (Fig. 13) is a small, bright (although somewhat damaged) specimen that looks as though it could have been reared, and pinned beside it in the drawer where it was originally placed by Dyar was a sample of a lichen, but without explanatory labels. The lichen was identified for me by Mason Hale, Department of Botany, National Museum of Natural History, as a species of the *Usnea longissima* group. Many lichens, including a similar *Usnea* species, occur conspicuously on the trunks and branches of trees at the type locality of *cyanympha*.

Remarks. The closest known relatives of *Cryphea cyanympha* are small, green species that have been collected in Cuba, the Dominican Republic and Puerto Rico. One of these is *Agriopodes jucundella* Dyar (1922: 10) (=*Cryphia jucundella* (Dyar), new combination) (Figs. 13, 25, 26) from Puerto Rico. *Bryolymnia huastea* Schaus (1940: 203) (Fig. 14), also from Puerto Rico, is almost certainly a junior synonym of *jucundella* and was misplaced in *Bryolymnia*. The type species of *Bryolymnia, Dacira roma* Druce of Mexico and Central America, is a larger, stouter moth with a well-developed corona and an incipient cucullus in the male genitalia, unlike species of *Cryphia* and other genera now placed in the Acronictinae. Although the holotypes of *jucundella* and *huastea* are both before me and appear conspecific, the former is a male and the latter a female, so that their genitalia cannot be compared. Two other similar species, apparently both undescribed, are represented by specimens in the U.S. National Museum from the Greater Antilles. One male from Cuba appears identical to *cyanympha* except that the valve lacks the clasper entirely.

Within the continental United States, *Cryphia cyanympha* is a distinctive, easily recognized species, but I illustrate for comparison and to support the generic placement the male genitalia of *C. viridata* and *C. jucundella*, as well as those of the type species of *Agriopodes, A. fallax*, which may be seen to differ conspicuously in the form of the juxta, valve, and aedeagus. A colored illustration of *fallax* was given by Covell (1984: pl. 26, fig 16).

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Fig. 1-6.   New Species of *Acronicta*. 1, *A. sinescripta*, holotype; 2, *A. sinescripta*, allotype; 3, *A. sinescripta*, ♀ paratype, Wedge Plantation, McClellanville, S. C., 20 Aug. 1968, D. C. Ferguson; 4, *A. kendallorum*, holotype; 5, *A. kendallorum*, ♂ paratype, same data as for holotype but emerged 27 June 1979; 6, *A. kendallorum*, allotype. About natural size.

Figs. 7-14. *Acronicta* and *Cryphia* species. 7, *A. perblanda*, holotype; 8, *A. perblanda*, allotype; 9, *A. perblanda*, ♂ paratype, Cartaret County, N. C., 30 Apr. 1974, J. B. Sullivan; 10, *A. perblanda*, ♂ paratype, Otter Slough Wildlife Area, Stoddard County, Mo., 28 May 1983, J. R. Heitzman; 11, *C. cyanympha*, paratype ♀, McClellanville, S. C., 26 Apr. 1970, R. B. Dominick & C. R. Edwards; 12, *C. cyanympha*, holotype; 13, *C. jucundella*, holotype, Puerto Rico; 14. *C. huastea*, holotype, Puerto Rico. About twice natural size.
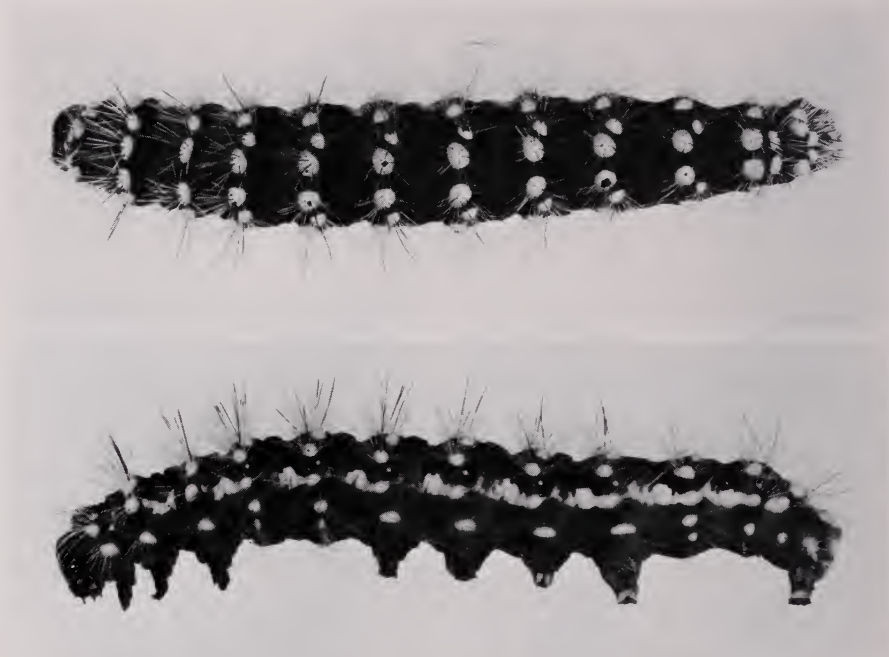
Fig. 15.   *Acronicta kendallorum*, paratype larva (preserved in alcohol). Dorsal and lateral views.
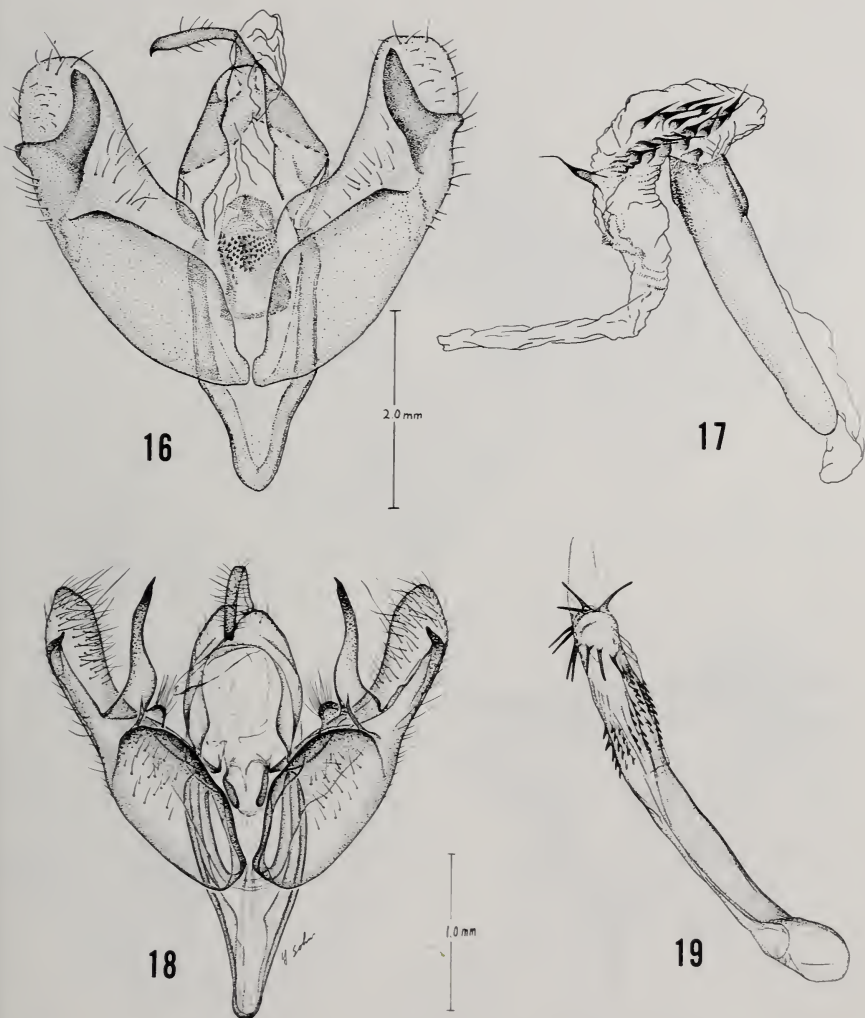
Figs. 16-19. *Acronicta* species, ♂ genitalia. 16, *A. sinescripta*, ♂ paratype, Highlands County, Florida, J. G. Franclemont slide No. 6751; 17, aedeagus of same specimen; 18, *A. perblanda*, ♂ paratype, Hilliard, Florida, D. C. Ferguson slide No. 1494 (Canadian Natl. Coll.); 19, aedeagus of same specimen.
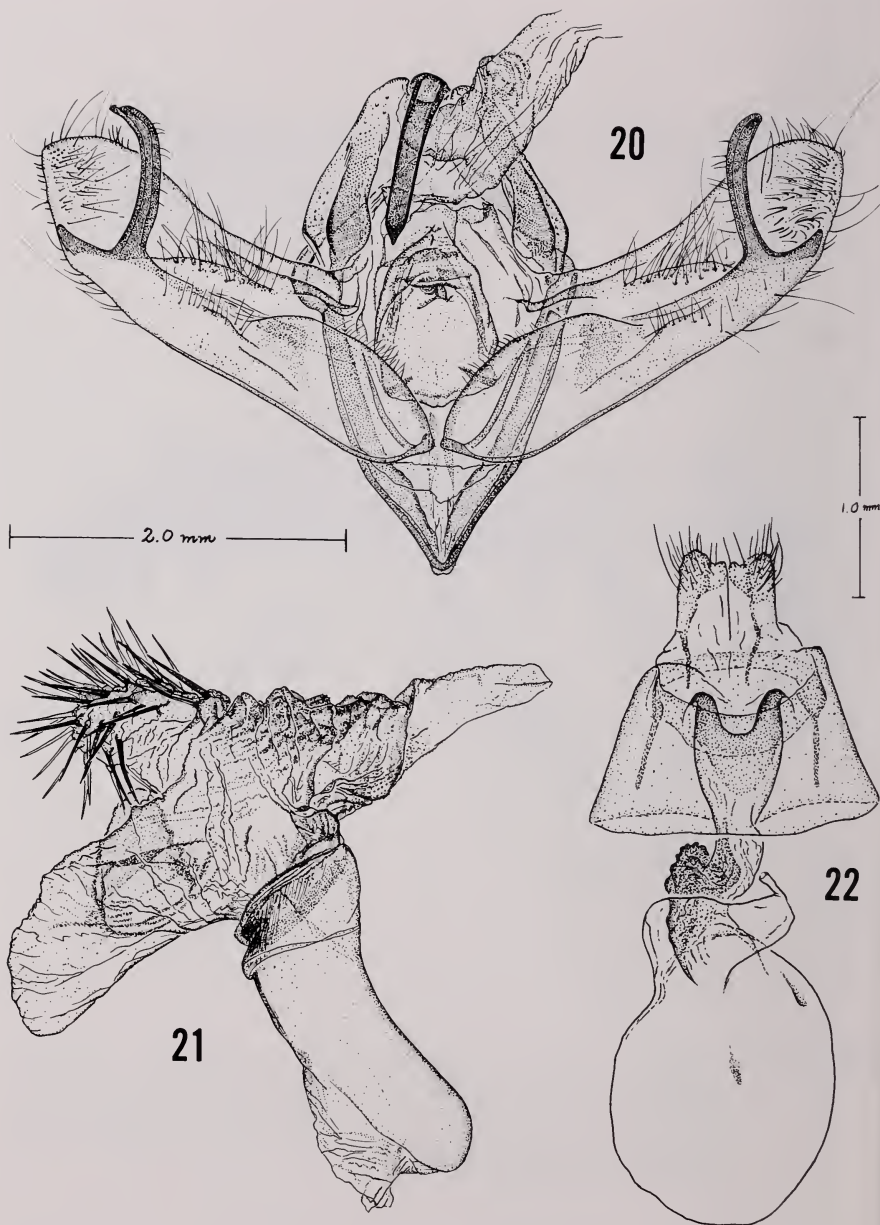
Figs. 20-22.   *Acronicta kendallorum* and *Cryphia cyanympha*, genitalia. 20, *A. kendallorum*, holotype, main part of ♂ genitalia. 21, aedeagus of same specimen. 22, *Cryphia cyanympha*, ♀ genitalia of paratype shown in Fig. 11.
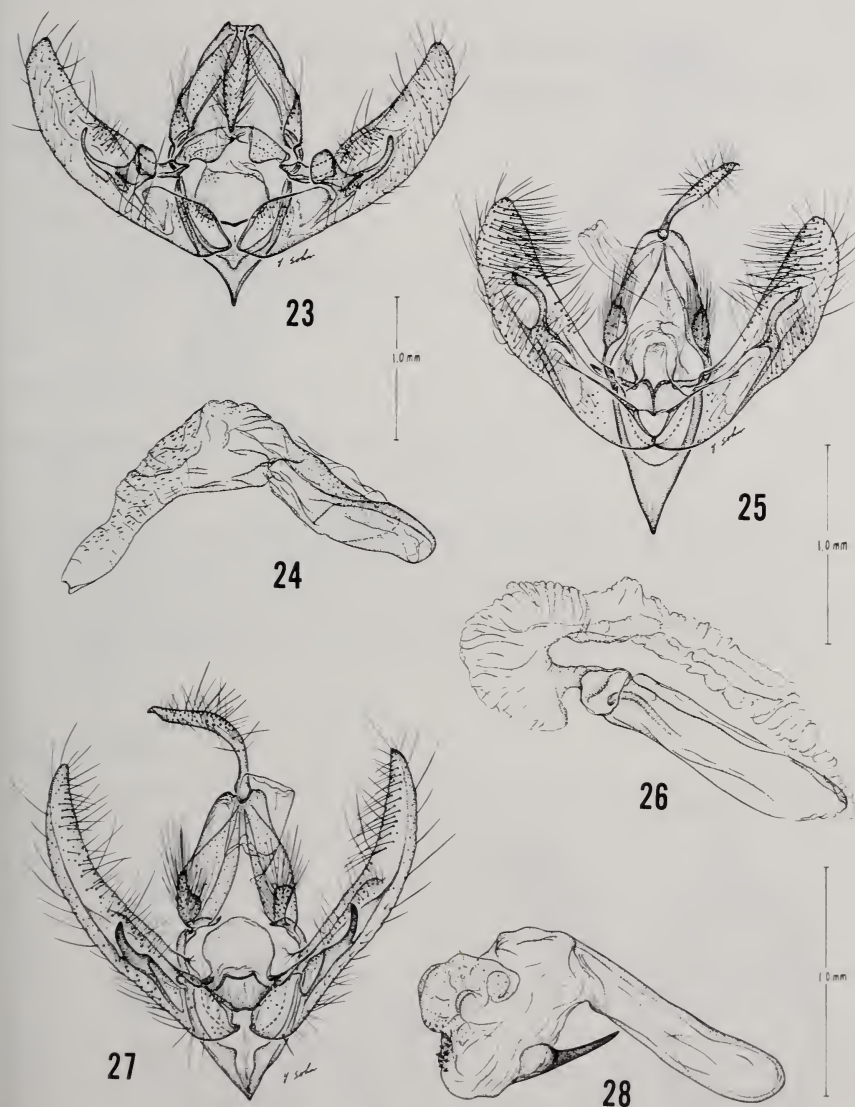
Figs. 23-28.   *Cryphia* species, male genitalia. 23, *C. viridata*, San Diego, California, USNM slide 52,177; 24, aedeagus of same specimen; 25, *C. jucun-della*, holotype; 26, aedeagus of same specimen; 27, *C. cyanympha*, paratype, McClellanville, S. C., USNM slide 52,101; 28, aedeagus of same specimen.
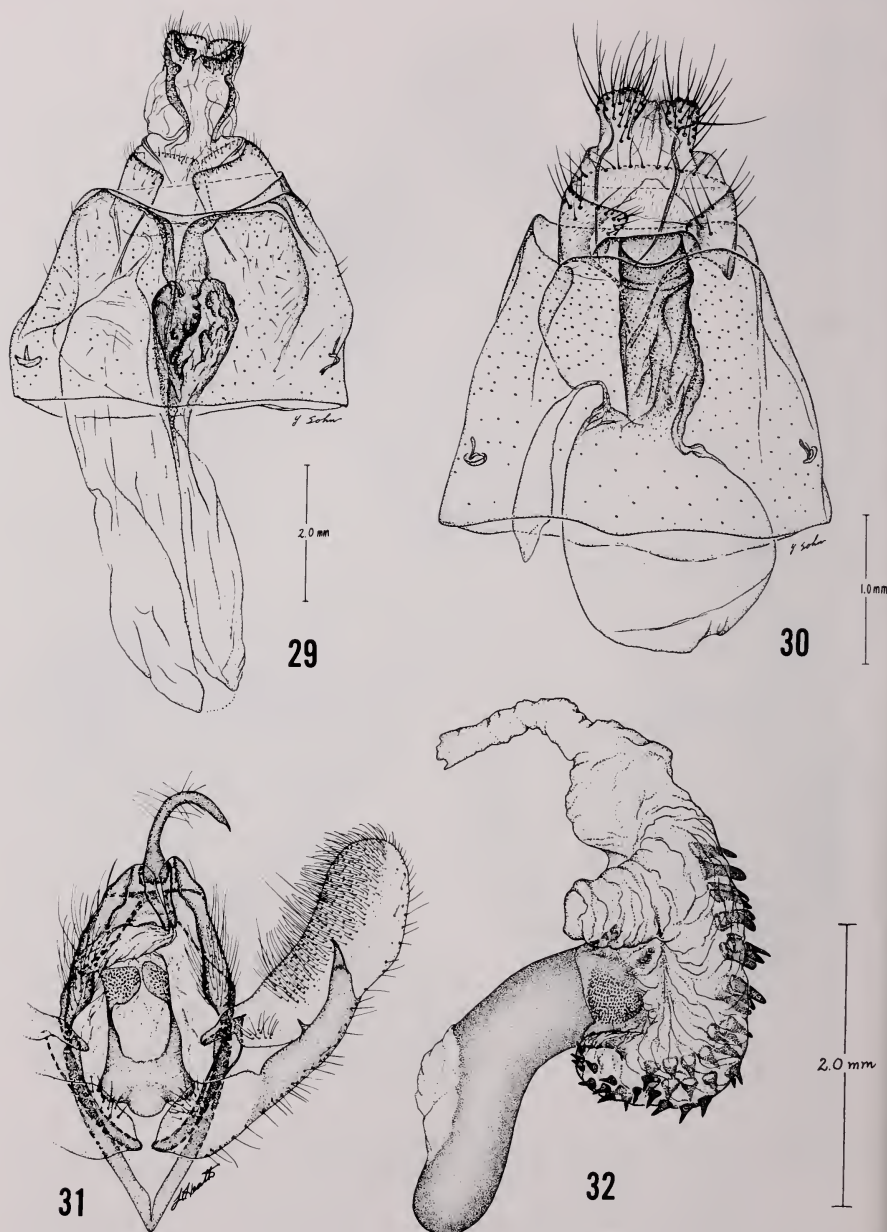
Figs. 29-32. *Acronicta* species, ♀ genitalia, and *Agriopodes fallax*, ♂ genitalia. 29, *A. sinescripta*, paratype, Gainesville, Florida, USNM slide 52,116; 30, *A. perblanda*, holotype; 31, *A. fallax*, Halifax County, Nova Scotia, USNM slide 52,106; 32, aedeagus of same specimen.

The identity of *Sphinx brunnus* Cramer and the taxonomic position of *Acharia* Huebner (Lepidoptera: Limacodidae)

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Abstract. The identity of *Sphinx brunnus* Cramer is established and *Acharia* Huebner is found to be a senior synonym of *Sibine* Herrich-Schaeffer. Taxa previously included in *Sibine* are listed. A lectotype for *Acharia brunna* is designated and illustrated. *Sibine zellans* Dyar and *S. berthans* Dyar are recognized as new junior synonyms of *Acharia brunna*.

Introduction

The identity of *Sphinx brunnus* Cramer has not been recognized since its description in 1777. Consequently, the placement of the genus *Acharia* Huebner has been uncertain since its publication. Huebner ([1819]) included *Acharia* in his "Stirp III. Glaucopen, *Glaucopes*" as "Coitus[=genus] 2", between "Coitus 1. *Aclytia* Huebner" and "Coitus 3. *Macrocneme* Huebner", both currently placed in the Ctenuchinae (Arctiidae). Kirby (1892: 166) included *Acharia* in the Charadrinae [=Ctenuchinae], after *Teucer* Kirby [=*Telioneura* Felder], and designated *brunnea* [a misspelling] as the type species, as Huebner originally also assigned another species, *Sphinx coras* Cramer, to the genus (*coras* is currently considered a synonym of *Phobetron hipparchia* (Cramer), also Limacodidae). Hampson (1898-1920), however, did not mention either *Acharia* or *brunnus* in his monographs on the Syntomidae [=Ctenuchinae] and Arctiidae. Therefore, *Acharia brunna* has remained unplaced until Fletcher and Nye (1982: 2) recently included it in the Limacodidae, as suggested to them by Becker.

These identity problems resulted from the inaccuracy of Cramer's figure and the unavailability of the type specimens to previous authors. Cramer's illustration (Fig. 1) depicts a uniformly brown-colored moth with falcate hindwings. No entomologist has ever located a specimen that matches the figure.

Sphinx brunnus was described from an unspecified number of speci-

mens from Surinam originally in the C. van Lennep collection. This collection passed on to Felder, then to Rothschild, and finally to the British Museum (Natural History) (BMNH). A specimen, presumably belonging to the type series, has been found at the BMNH. We examined this specimen (Fig. 2), have figured its genitalia (Fig. 4), and designate it here as the lectotype. The specimen matches Cramer's illustration very well, except for the transluscent areas along the hindwing termen (Fig. 2). There are two reasons why no subsequent specimen has been found to match either Cramer's illustration or the type specimen. First, none of the plain brown specimens in collections have falcate hindwings

Fig. 1.   Reproduction of figure 147c from Cramer, 1777.
Fig. 2.   Lectotype male of *Acharia brunna* (BMNH) (forewing length about 14 mm).
Fig. 3.   Holotype male of *Sibine zellans*, from Pará [=Belém], Brazil (USNM 40684).

as shown by Cramer (Fig. 1). Secondly, the type specimen was painted to match the figure, and the paint has partially pealed off (especially along the hindwing margins), giving the impression that the species belongs to the *auromacula* group of the genus *Sibine* herrich-Schaeffer, which have the hindwings partially transluscent and with a falcate termen. However, none of the species belonging to the *auromacula* group (*auromacula* Schaus, *intensa* Dyar, *barbara* Dyar, *sibinides* Dyar, and *blanda* Dyar) have plain brown forewings. They all have two well defined white dots, a round one below the cell, and an elongate one beyond the cell apex, crossing R3+R4 and R5.

In the extensive series of *Sibine* in the National Museum of Natural History (USNM) and the Becker collection, we have found only two males which have plain dark brown wings that match the lectotype of *Acharia brunna*. These are the holotype of *S. zellans* Dyar (Fig. 3) (Pará [=Belém], Brazil, [no date], A.M. Moss) and a syntype of *S. berthans* Dyar (Villa Rica [=Villarrica], Paraguay, March 1926, F. Schade). *S. berthans* was described from two syntypes, a male and a female from the same locality, both in USNM. We hereby designate the male as lectotype. Without revision of the genus, we cannot be sure that the female paralectotype is conspecific with the lectotype, and do not treat it further here.

The external margin of the hindwings is straight in *Sibine zellans*, but slightly convex in *S. berthans*. However, the genitalia of both are identical and match perfectly those of *Acharia brunna*. The only differences mentioned in the original descriptions (Dyar, 1927: 547) were that *berthans* has the "wings rather less pointed" and the "spines of the penis [=cornuti of aedoeagus] are finer and more numerous than in *zellans*." We are convinced that they are all conspecific. We regard the differences in wing shape as individual or local variation, and the slight differences in cornuti as insignificant. Although it is widely distributed (Surinam, through the Amazon Basin, into Paraguay), apparently *brunna* does not readily come to light and is therefore rare in collections.

Dyar (1935) reviewed the species of *Acharia* (as *Sibine*), and gave a key with poor quality illustrations of wing surfaces. The genus, which includes several agriculturally important species, needs revision. Without a modern revision of all the species, it is not possible to assess the significance of the morphological variation discussed above.

Checklist

Except for *berthans* and *zellans*, which are newly synonymized under *brunna*, the taxa are listed as they presently stand in the literature. We expect that examination of type material of the older names, as well as newly accumulated material in collections, will result in many taxonomic changes. Forbes (1942) has suggested several taxonomic changes, but they should not be adopted without examination of the relevant types.
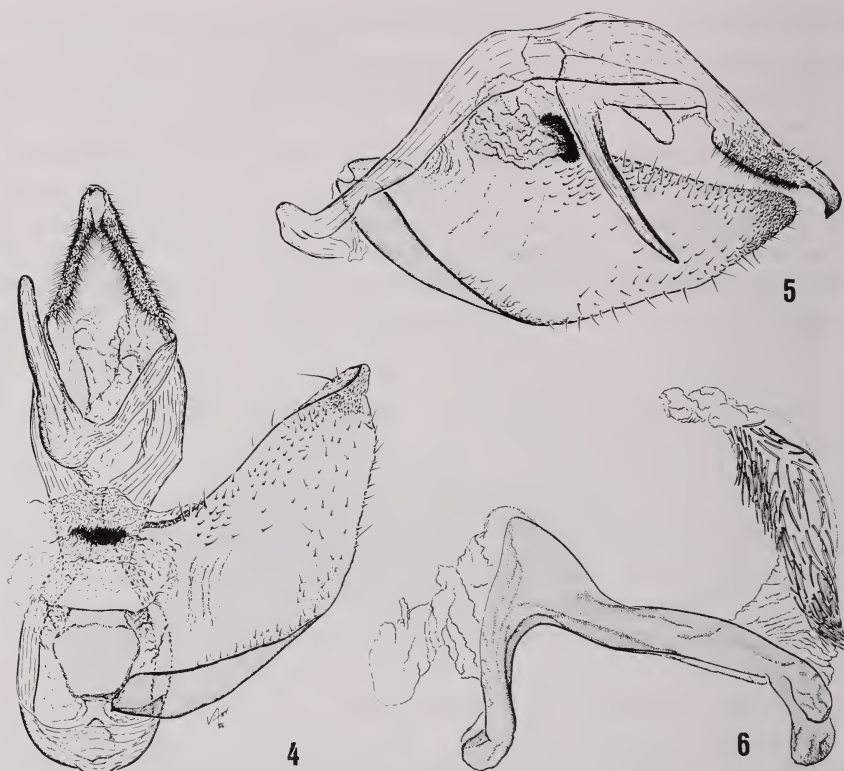
Acharia Huebner, [1819]

Fig. 4-6.   Male genitalia of lectotype of *Acharia brunna*: 4: ventral view (manica not shown); 5: lateral view, 6: aedoeagus, with vesica everted.

Sibine Herrich-Schaeffer, 1855, n. syn.
Empretia Clemens, 1860, n. syn.
Eupretia Walker, 1865, misspelling
Eupalia Walker, 1866, n. syn.
Episibine Dyar, 1898, n. syn.

affinis (Moeschler, 1883) (Sibine) n. comb.
alicians (Dyar, 1935) (Sibine) n. comb. [as subspecies of nitens]
apicalis (Dyar, 1900) (Sibine) n. comb.
auromactila (Schaus, 1896) (Sibine) n. comb.
ausa (Dyar, 1935) (Sibine) n. comb. [as subspecies of stimulea]
barbara (Dyar, 1905) (Sibine) n. comb.
blanda (Dyar, 1935) (Sibine) n. comb.
bonaerensis (Berg, 1878) (Streblota) n. comb.
brunna (Cramer, 1777) (Sphinx) n. comb.
    berthans (Dyar, 1927) (Sibine) n. syn., n. comb.
    zellans (Dyar, 1927) (Sibine) n. syn., n. comb.
clarans (Dyar, 1927) (Sibine) n. comb.
didactica (Dyar, 1927) (Sibine) n. comb.
differentiata (Bryk, 1953) (Sibine) n. comb. [as subspecies of joyceans]

dorans (Dyar, 1927) (Sibine) n. comb.
eucleides (Dyar, 1905) (Sibine) n. comb.
extensa (Schaus, 1896) (Sibine) n. comb.
francescans (Dyar, 1927) (Sibine) n. comb.
fusca (Stoll, 1780) (Phalaena) n. comb.
gertrudans (Dyar, 1927) (Sibine) n. comb.
geyeri (Fletcher, 1982) repl. name (Sibine) n. comb.
    nesea (Geyer, [1833]) (Streblote) n. comb.
giseldans (Dyar, 1927) (Sibine) n. comb.
helenans (Dyar, 1927) (Sibine) n. comb.
horrida (Dyar, 1905) (Sibine) n. comb.
hyperoche (Dognin, 1914) (Sibine) n. comb.
intensa (Dyar, 1905) (Episibine) n. comb.
iolans (Dyar, 1927) (Sibine) n. comb.
joyceans (Dyar, 1927) (Sibine) n. comb.
laberia (Dyar, 1935) (Sibine) n. comb.
laurans (Dyar, 1927) (Sibine) n. comb.
lophostigma (Dognin, 1910) (Sibine) n. comb.
megasomoides (Walker, 1866) (Eupalia) n. comb. [currently subspecies of
   rufescens]
minuscula (Bryk, 1953) (Sibine) n. comb. [as subspecies of auromacula]
modesta (Cramer, 1777) (Phalaena) n. comb.
nesea (Stoll, 1780) (Phalaena) n. comb.
    vidua (Sepp, [1848]) (Phalaena) n. comb.
    fumosa (Walker, 1855) (Nyssia) n. comb.
nitens (Dyar, 1905) (Sibine) n. comb.
norans (Dyar, 1927) (Sibine) n. comb.
ophelians (Dyar, 1927) (Sibine) n. comb.
pauper (Dyar, 1918) (Sibine) n. comb.
permessa (Dyar, 1918) (Sibine) n. comb.
priscillans (Dyar, 1927) (Sibine) n. comb.
quadratilla (Dyar, 1935) (Sibine) n. comb.
quellans (Dyar, 1927) (Sibine) n. comb.
reletiva (Dyar, 1927) (Sibine) n. comb.
rollans (Dyar, 1927) (Sibine) n. comb.
rufescens (Walker, 1855) (Nyssia) n. comb.
    determinata (Walker, 1865) (Nyssia) n. comb.
    plora (Schaus, 1896) (Sibine) n. comb.
    pallescens (Dognin, 1901) (Sibine) n. comb.
sabis (Dyar, 1935) (Sibine) n. comb.
sarans (Dyar, 1927) (Sibine) n. comb.
sibinides (Dyar, 1905) (Episibine) n. comb.
stimulea (Clemens, 1860) (Empretia) n. comb.
    ephippiatus (Harris, 1869) (Limacodes) n. comb.
subalbicans (Dyar, 1935) (Sibine) n. comb.
tontineans (Dyar, 1927) (Sibine) n. comb.
trimacula (Sepp, [1848]) (Phalaena) n. comb.
varia (Walker, 1855) (Nyssia) n. comb.
violans (Dyar, 1927) (Sibine) n. comb
ximenans (Dyar, 1927) (Sibine) n. comb.

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The Life History of *Hemileuca magnifica* (Saturniidae) With Notes on *Hemileuca hera marcata*

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Abstract. *Hemileuca magnifica* is a diurnal saturniid inhabiting Climax Sagebrush Associations in southern Colorado and northern New Mexico. The larval host is exclusively *Artemisia tridentata* in Costilla County, Colorado and northern Taos County, New Mexico. The Albuquerque, Bernalillo County, New Mexico colony is found on *A. filifolia*. The species has a two-year life cycle, overwintering first as ova and the second winter as pupae. The ova are deposited in rings typical of *Hemileuca* species. The young larvae feed gregariously and as they mature, disperse widely. Observations of insect parasitism and avian predation are reported.

Introduction

Until recently, *Hemileuca magnifica* (Rotger) (Saturniidae) was represented in private and museum collections by very few specimens (Ferguson 1971) and virtually nothing was known of its life history. The present paper provides new information on habitat, behavior, and biology. *Hemileuca magnifica* was considered a subspecies of *H. hera* by the original author and Ferguson (1971), but more recently the moth was given full specific rank (Ferguson 1983).

Discussion

Habitat

Hemileuca magnifica is a cryptically colored black, white and orange saturniid of moderate size inhabiting the Upper Sonoran Life Zone in

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southern Colorado and northern New Mexico. The Upper Sonoran Life Zone, which includes the Sagebrush-Pinyon-Juniper Belt, extends from at least Colorado and Utah south to central Arizona and New Mexico. The altitudinal range of this zone is from about 1,370 to 2,280 m and its limits vary with and are influenced by differences in exposure, soil, and moisture conditions (Gregg 1963, Patraw and Janish 1977).

Sagebrush, (*Artemisia tridentata* Nuttall: Compositae) is found at elevations between 1,820 and 2,500 m and ranges through western North America from South Dakota to British Columbia and south to New Mexico, northern Arizona and Baja California and is, therefore, not restricted to the Upper Sonoran Life Zone. The plant can cover vast areas to the almost total exclusion of other plant species and can grow well over two m in height in conditions of favorable soils and abundant precipitation, but one m or less is normal (Coyle and Roberts 1975, Elmore and Janish 1976, Gregg 1963, Kearney and Peebles 1942, Patraw and Janish 1977, Rydberg 1906, Tidestrom 1925, Wiggins 1980, Wooton and Standley 1915).

Artemisia tridentata is the dominant shrub of the Climax Sagebrush Association southern San Luis Valley, Costilla County, Colorado where most of the work reported in this study took place. Occasional associated plant species within this study area include rabbitbrush (*Chrysothamnus* sp.: Compositae) and saltbush (*Atriplex* sp.: Chenopodiaceae) (Lamb 1975). The Climax Sagebrush Association at Albuquerque, New Mexico is dominated by *Artemisia filifolia* Torrington.

Seasonal temperatures in the study area range from 35°C during July and August to extremes of −35°C and lower in December and January. Annual precipitation averages less than 20 cm (Colorado Climate Center, pers. comm.) with occasional summer thunderstorms. The majority of moisture, however, is received as winter snows.

Range

Hemileuca magnifica is associated with Climax Sagebrush Associations (Fig. 1) at elevations between 2,000 and 2,500 m. In Costilla County, Colorado the known range of *H. magnifica* extends from just north of Fort Garland south through Mesita (type-locality) and Jaroso. It extends further south in New Mexico through Taos County to Albuquerque, Bernalillo County and then west to just northeast of Pintado, McKinley County (Jim Coleman, pers. comm., and Ferguson 1971). Thus, *H. magnifica* inhabits a limited, roughly triangular area on the border of northern and northwestern New Mexico and south central Colorado. However, Townsend (1893) stated that on 25.VII. 1892 he observed a number of large brownish and blackish *Hemileuca* larvae feeding on *A. filifolia* east of Navajo Springs, Arizona. It is reasonable to believe the species Townsend observed were *H. hera hera* (Harris) or *H. magnifica*. Navajo Springs, Apache County, Arizona shares the same Great Basin influence as Pintado, McKinley County, New Mexico (Martin and Hutchins 1980), which is the westernmost known locality

Fig. 1. Typical climax Sagebrush habitat which supports *Hemileuca megnifica*.

for *H. magnifica*. As discussed below, populations of *H. magnifica* and *H. h. hera* are not known to be sympatric nor parapatric.

Biology

The *Hemileuca hera* group is composed of three taxa, *H. h. hera, H. h. marcata* (Neumoegen), and *H. magnifica*, which have long been associated with sagebrush communities (Holland 1903, McFarland 1974, Packard 1914, Ferguson 1971, Furniss and Carolin 1977). Recently, *H. h. hera* in California has been shown to prefer *A. tridentata* as host, although when larval populations are dense, various species of *Lupinus* (Mimosoideae) and *Eriogonum* (Polygonaceae) are also used (Tuskes 1984). The population of *H. magnifica* in the vicinity of Albuquerque, New Mexico feeds only on *A. filifolia* (Jim Coleman, pers. comm.) while those of Taos County, New Mexico and Costilla County, Colorado feed exclusively on *A. tridentata* as does the colony of *H. h. marcata* in Klamath County, Oregon (Melvin Parker, pers. comm.).

It is noteworthy that *H. magnifica* is not distributed uniformly throughout all suitable range, but seems to be highly localized in concentrated populations, as is *H. h. hera* in California (Tuskes, pers. comm.). The preferred habitat seems to be areas where the host is growing in sandy-loamy-clay soils and is fairly tall, dense and lush. Coarse gravelly areas, where the host plant is shorter and less fully developed, do not appear to support populations of *H. magnifica*. Even where lush and stunted sagebrush communities are adjacent, the stunted areas are devoid of *H. magnifica*. Patrolling (mate seeking)

males stay within the more lush habitats and larvae are found only in such areas.

Adults in Jaroso are on the wing from early August to late September with the main flight in late August. Males fly from approximately 1100 to 1500 hours (Mountain Daylight Time). Ovipositing females may be on the wing until 1800 hours. Adults hatch from 0900 to 1200 hours emerging from the pupa and climbing a short way into nearby vegetation, usually *A. tridentata*, where they expand and harden their wings which takes about an hour. As soon as males harden their wings they fly off in search of a mate. It is to the advantage of male saturniids to cover as much suitable habitat as quickly as possible in their search for potential mates, which is why they are such wide ranging and active fliers (Janzen 1984). It would appear males flying in late afternoon are those that have been unsuccessful in locating a virgin female earlier in the day and are still actively seeking a mate, or have mated earlier in the day and are seeking another mate.

Females start emitting pheromone as soon as their wings are hardened and usually do not fly until after copulation. As discussed by Tuskes (1984) for *Hemileuca* in general, newly emerged females usually remain on lower stems of the plant while emitting pheromone. Mating requires one to three hours. After separation, the females seldom fly to deposit the first egg ring but, instead, crawl up the plant to form a ring of cream colored eggs on an apical shoot of the host. The rings are typical of the genus *Hemileuca*. The first ring contains ca. 50 to 75 ova. During the next few days, the female deposits several additional egg rings, but each contains a smaller number of 30 to 35 ova. The female may deposit 100 to 200 ova during her life of five to seven days. Ova normally overwinter the first year.

Although theoretically equal in numbers to males, females are uncommonly encountered. It would appear that females which have mated need not range far seeking suitable hosts for oviposition. After ovipositing, which takes anywhere from 30 minutes to more than an hour, the female may or may not immediately fly again in search for another host. Our observations indicate the female may perch and rest for several hours or until the next day depending on her burden of ova, age, strength and condition.

Females mate once, males may mate several times as opportunity provides. Males searching for pheromone plumes emitted by virgin females search exactly as described by Collins and Tuskes (1979), Collins and Weast (1961), and Janzen (1984). The males fly corsswind at rapid speed searching for pheromone plumes emitted by females. Upon encountering a plume they follow it upwind to the female by an ever decreasing series of lateral oscillations. When males are from one to two m from the female, flight slows and is more direct. When males are less than one m from the female, they fly very slowly and frequently hover within a few cm of the female before landing.

Our observations indicate the male crosswind flight often exceeds

Fig. 2. Adult male *H. magnifica* perched for the night on *Artamisia*. P.

400 m. If no plume is encountered the male drops downwind several hundred m and begins another crosswind search pattern. Patrolling males generally cruise widely just over the tops of the sagebrush and seem to prefer draws, washes and saddles, perhaps using these topographic features as natural flyways. A single caged pheromone-emitting female may attract hundreds of males within a few hours.

After the daily flight is over, adults, especially males, tend to perch on the high exposed tips of plants where they spend the night (Fig. 2). Tuskes (pers. comm.) observed similar behavior in populations of *H. eglanterina* (Boisduval), *H. nuttalli* (Strecker), and *H. h. hera* in east Sierra country in California. Approximately one hour after sunrise of the next morning they position themselves in an easterly, southeasterly or southern orientation with the dorsal surface fully exposed to the sun in order to sufficiently warm to begin the day's activities.

In Jaroso, Colorado ova hatch from mid to late June. In Albuquerque, New Mexico ova hatch from early to mid May (Jim Coleman, pers. comm.). Larvae bear urticating spines and are gregarious until mid to late third instar when they disperse widely. More mature larvae generally prefer apical, succulent growth. During the day these older larvae tend to gravitate to this exposed growth and are easily seen (Fig. 3). Larvae were also observed in shadier portions of the host, probably shifting between these two areas as a means of thermoregulation (see Capinera et al. 1980). During the night larvae retreat to the interior of the host where their color patterns provide excellent camouflage.

Fig. 3.   Last instar larva of *H. magnifica in a natural day-time feeding position.*

Larvae reared indoors on cut host do poorly. Ferguson (1971) stated that *H. h. hera* larvae have successfully been reared in screened cylinders placed in sunlight for an hour or so each day. *Hemileuca magnifica* larvae can be reared indoors but require spacious airy conditions and the radiation of a "Gro-Light" (Tuskes, pers. comm.). They do best if reared outdoors on living hosts, but will mature indoors on cut food if it is fresh. The later instars cannot stand crowding and will die if crowded. These findings are consistent with those of McFarland (1974) and Smith (1974).

Pupation is a few cm under the soil surface without any kind of cocoon. The pupae normally overwinter for a single year, but individuals holding over for two or more years are known.

Adult Coloration

The black, white and orange colors of *H. magnifica* adults are an excellent camouflage while they are perched deep inside sagebrush plants, especially during the most vulnerable time of expanding and hardening their wings. If the moths are distasteful to birds as Ferguson (1971) suggests, then moths of this genus would be interesting inasmuch as they are cryptic while resting yet aposematic in flight. The black and white of wings blend well with the light and shadows within the host and help to break up the adult outline. The orange tufts and rings on the body are a very close match to an orange lichen (*Xanthoria polycarpa* (Ehrh.) Olir.: Teloshistaceae) found commonly on sagebrush stem and trunk bark, especially in the Jaroso area. The evolution of

highly developed orange patches and rings on adult *H. magnifica* may be directly related to the lichen. While in repose within the sagebrush plant the orange color further helps to conceal the adults and may contribute to reduced predation pressure.

Parasitoids and Predators

A group of 50 *H. magnifica* larvae ranging in age from 3rd instar to mature were collected on *A. tridentata* 24. VIII. 1985 at Jaroso, Colorado. The following parasitoids were found.

Diptera. *Exorista* sp. (Tachinidae); medium sized flies, of which several specimens were reared. *Chetogena* sp. (Tachinidae); smaller sized flies, of which several specimens were also obtained. The species are not presently identifiable, according to N. E. Woodley who determined them. Arnaud (1978) cited no parasitic tachinid records for *H. magnifica*.

Hymenoptera. *Microdontomerus fumipennis* Crawford (Torymidae), determined by E. E. Grissell. These small wasps with prominent ovipositors are known to attack several hosts (Krombein et al. 1979, Peigler 1985). Numerous wasps emerged from a single host.

Cotesia electrae (Viereck) (Braconidae), determined by P. M. Marsh, formerly classified in the genus *Apanteles*. (*Apanteles electrae* has been recorded as a parasitoid of a *Hemileuca* species in Texas [Peigler 1985], *Agapema galbina* [Collins and Weast 1961], *H. h. hera* and other saturniids, especially Hemileucinae [Krombein et al. 1979] in western North America.)

When the *C. electrae* larvae are mature, they exit the host and spin silken cocoons directly on the host body surface (Borror and DeLong 1970 [as *Apanteles*]). A population of 10 to 20 parasitic *C. electrae* larvae per parasitized *H. magnifica* larva host is common.

Voucher material of *Chetogena* and *Microdontomerus* were deposited in the U. S. National Museum of Natural History, and *Exorista* and *Cotesia* in the Los Angeles County Museum of Natural History.

Jim Coleman (pers. comm.) has reported robins (*Turdus migratorius* Ridgeway) occasionally feeding on mature *H. magnifica* larvae in the Albuquerque colony.

Larva Description

A description of a mature *H. magnifica* larva (Fig. 4) follows based on living material from Jaroso, Colorado. There usually are six instars although seven is not uncommon (see Lemaire 1979: 231, footnote).

DESCRIPTION OF MATURE LARVA OF *HEMILEUCA MAGNIFICA*

HEAD: Lustrous black to reddish brown with abundant white secondary setae; diameter 4.5-5.0 mm. **BODY**: Length (including head) 60.0-72.0 mm: width 9.0-11.0 mm. Ground color dark brown approaching black, rarely tan to light brown. Body with four pairs of off-white lines which may be reduced to a series of inconspicuous dashes. Subspiracular line most developed, broad, and quite pronounced, running through subspiracular and subdorsal scoli and

Fig. 4. Last instar larva of *H. magnifica*.

variably developed, but always less than subspiracular line. Subdorsal line between subdorsal and dorsal scoli, and significantly reduced or absent. Dorsal line between dorsal (rosette) scoli, reduced to narrow white dashes or dots, if present. Ventral scoli present on pro-, meso-, and metathorax and abdominal segments one, two, seven and nine. Dorsal scoli present as two rows of short dull yellow rosettes with black tips, on metathorax and next seven abdominal segments; on abdominal segment eight a median rosette; on pro- and mesothoracic segments rosettes containing larger black scoli resembling subdorsal and spiracular ones. Subdorsal and lateral scoli long, black, and yellow tips on branches. Numerous white secondary setae over entire body surface. True and prolegs black, feet white on inner side. Spiracles black. Abdominal and especially thoracic segments with white dots or markings ventrally, anterior to each proleg or true leg.

Since no descriptions of the early stages of *H. hera marcata* have been published, we offer the following description based on a mature larva in alcohol. The specimen was collected as a first instar larva on *A. tridentata* at Klamath Falls, Klamath County, Oregon by Melvin Parker and reared to maturity on *A. tridentata* by Dean Swift in Jaroso, Costilla County, Colorado.

DESCRIPTION OF MATURE LARVA OF *HEMILEUCA HERA MARCATA* **HEAD**: Lustrous black with abundant white secondary setae; diameter 4.0 mm. **BODY**: Length (including head) 55.0 mm; width 7.0-9.0 mm. Ground color purplish brown. Body with four pairs of off-white lines. Subspiracular line most developed, broad, running through subspiracular scoli, with dark evaginations from ventral edge. Lateral line between subspiracular and subdorsal scoli, closer to latter, prominent and unbroken, but only half as thick as subspiracular line. Subdorsal line between two aforementioned lines

in thickness, unbroken. Dorsal line barely visible, except on thoracic segments, running between dorsal scoli. Ventral scoli present on pro-, meso-, and metathorax and abdominal segments one, two, seven and nine. Dorsal scoli present as two rows of short dull yellow rosettes with black tips, on metathorax and next seven abdominal segments; on abdominal segment eight a median rosette; on pro- and mesothoracic segments (and three on abdominal segment nine) rosettes containing larger black scoli resembling subdorsal and lateral ones. Subdorsal and lateral scoli long, black, with yellow tips on branches. Numerous white secondary setae over entire body surface. True legs black, prolegs white with dark patches on outer sides. Spiracles black. Ventral surface predominantly off-white, with a few small dark median patches on each segment.

Preserved mature larvae of *H. magnifica* and *H. h. marcata* have been deposited in the Los Angeles County Museum of Natural History.

Diagnosis

Based on our above observations of mature larvae of *H. magnifica* and *H. h. marcata* and the description of *H. h. hera* by Tuskes (1984) plus a color slide of *H. h. hera* which he kindly sent to us, we are able to make the following brief comparisons. The larva of *H. h. hera* has a slender yet conspicuous subspiracular stripe, but less developed than the lateral one; in *H. h. marcata* and *H. magnifica* this ventralmost stripe seems to be widest and the most conspicuous. The dorsal rosette scoli of *H. h. hera* appear to be dull yellow, like the ones in *H. magnifica* and *H. h. marcata*. The ventral surfaces of *H. h. hera* and *H. magnifica* are predominantly blackish, whereas *H. h. marcata* is mainly whitish throughout the ventral area. As would be expected due to the size of the imagines, the larva of *H. magnifica* is larger than those of the other two.

Comparison of *H. h. hera*, *H. h. marcata* and *H. magnifica* convinces us that these three taxa form a compact group, or a subgroup within the *eglanterina* group of Tuskes (1984, Table 1). The adults of these three differ from their nearest relatives (viz *H. nuttalli* and *H. eglanterina*) by lacking yellow or orange scales on the wings. The *hera* subgroup also differs from the other members of the *eglanterina* group by being almost exclusively feeders on sagebrush.

As mentioned above, Ferguson (1983) elevated *H. magnifica* to full specific status; the same author (Ferguson 1971) earlier speculated that both *H. magnifica* and *H. h. marcata* could be full species distinct from *H. h. hera*. Since subspecies by definition should have ranges that overlap or at least are in contact, and show blending of characters, we consider it significant that no such zones are known for *H. h. hera* and *H. magnifica*. These two species are allopatric as far as known. Any pair of full species could be either allopatric or sympatric, but if two taxa are subspecies, they should show blending in a parapatric pattern. As discussed earlier, the status of *H. h. hera* and *H. h. marcata* is less certain.

Presently the response of each species males to calling females of the other taxon is unknown. Tuskes (1984) discussed a blend zone of *H. h.*

hera and *H. h marcata* and described what appears to be intergrade adults. He referred to *H. h. marcata* as a "form" but did not state whether the *H. h. hera* population in California contacts the *H. h. marcata* in Oregon, or if the two populations are disjunct. The "*H. h. marcata* population in Oregon, or if the two populations are disjunct. The "*H. h. marcata*" he figured from California is not as extreme in reduction of black markings as in specimens of true *H. h. marcata*. backcrosses and sibmatings could be reared. Such hybrid work may answer such questions as the nature and degree of phenotypic variation of hybrid individuals, ova fertility and fecundity, survival and viability of hybrid individuals throughout development (which is directly related to phylogenetic divergence), and isolating mechanisms (see Peigler and Williams 1984).

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Opinion. Opinion is intended to promote communication between lepidopterists resulting from the content of speculative papers. Comments, viewpoints and suggestions on any issues of lepidopterology may be included. Contributions should be as concise as possible and may include data. Reference should be limited to work basic to the topic.

Are We Studying Our Endangered Butterflies to Death?

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A number of studies suggest that handling has adverse effects on butterflies. Singer and Wedlake (1981), for instance, were able to recapture only 2% of the *Graphium sarpedon* that had been captured, marked, and released on a riverside beach in Sarawak. Subsequently, they were able to mark the swallowtails without handling.

"The procedure employed was to crawl towards the insects extremely slowly, taking several minutes to reach them. On the first occasion that this was tried, the marker pen was held in an outstretched hand, but it was found to have dried out by the time it reached the feeding butterflies. Subsequently we wormed our way up the beach on our stomachs with both hands outstretched, so that we could delay uncapping the pen until after its arrival among the butterflies."

After using these methods, Singer and Wedlake found that recapture rates soared to 21%. Morton (1984) in a temperate zone study likewise found that marking the lycaenids *Polyommatus icarus* and *Lysandra coridon*, without handling, also resulted in increased recapture rates.

Direct impact of handling on butterfly behavior and longevity, however, has been difficult to document. Powell (pers. com.) has observed that freshly emerged adults of the endangered Lange's metalmark butterfly (*Apodemia mormo langei*) assume their nocturnal resting position when marked immediately after emerging from their pupae. Some individuals retain this position for extended periods which could subject them to higher rates of predation. Reid (1985 and pers. comm.) found that handling of the endangered mission blue butterfly (*Plebejus icarioides missionensis*) results in about 10% mortality. He has for that reason discontinued the use of mark-recapture techniques in long-term studies on San Bruno Mountain. Many field workers suggest that mark-recapture methods probably should never be employed with small-winged, swift-flying species, for example the threatened Pawnee

montane skipper (*Hesperia leonardus montana*) presently under study in Colorado.

Despite this mounting evidence that many butterflies exhibit greatly disturbed behavior or suffer physical damage from marking and recapture, mark-recapture remains one of the initial steps in nearly every conservation effort focussing on butterflies. This is especially ill-advised because the data obtained from such studies rarely are useful in the protection of endangered species. For instance, mark-recapture studies and intensive statistical analysis have revealed few differences in population parameters between the gravely endangered bay checkerspot butterfly (*Euphydryas editha bayensis*) and the widespread chalcedon checkerspot (*Euphydryas chalcedona chalcedona*) on Jasper Ridge Biological Preserve at Stanford University (Murphy, et al. 1986). The study suggested that "new approaches both to mark-recapture analysis and the study of endangered species are needed to generate more useful information concerning the conservation status of invertebrate populations." Murphy et al. further conclude that methodologies which minimize physical damage to butterflies and their habitats should be emphasized when studying endangered or threatened species.

The limits of distributions and relative densities of butterflies within their habitats constitute the critical information usually sought by conservation biologists. This information nearly always can be ascertained through simple observation and use of a low impact "sampling" technique such as that of Pollard (1977), which involves repeatedly walking transects while recording the number of butterflies observed. The purported advantage of mark-recapture techniques over transect observations lies in the estimate of absolute (rather than relative) population sizes which may be generated from field data. But this advantage usually is moot since endangered butterflies are virtually always restricted to small habitat patches where population sizes are small. Little practical value is gained from establishing that populations that are obviously small are indeed small.

Two additional problems are prevalent when mark-recapture techniques are used to derive population size estimates for conservation studies. First, the variances associated with these estimates are often as large as the population estimates themselves. The only way to reduce that variance is to increase the handling, marking, and recapturing of the endangered butterflies. Second, exact population size is relatively unimportant when developing conservation agendas. For example, the entire two acres of habitat owned by Chevron Oil, in Southern California, must be protected and maintained free of alien plant species to ensure the persistence of the El Segundo blue butterfly, whether 100, 300, or 1,000 individuals are present in any given year.

If mark-recapture studies offer little guidance in conservation efforts, why then are they allowed—and even promoted? The answer may rest in the fact that most studies are commissioned in response to govern-

ment regulations which require private land developers to assess the potential impact of proposed habitat disturbance to endangered species. The lead agency in these situations is either the United States Fish and Wildlife Service or a state agency with a similar mandate for species protection. Limited by tight budgets and small staffs emphasizing fish and game resource management, these agencies often must seek advice from outside "experts," especially on matters pertaining to invertebrate conservation. Many consultants take advantage of this situation to promote more labor-intensive (read 'more expensive') field methodologies, such as mark-recapture studies, when simpler approaches are adequate to achieve most conservation objectives.

A particularly egregious example is a recent study involving the federally protected Smith's blue butterfly (*Euphilotes enoptes smithi*) on Marina State Beach in Monterey County, California (Arnold, 1986). This study proposed no new approach to the management of this endangered butterfly, yet it potentially subjected a population to severe impacts from handling. Nominally trained "students" were used to mark more than 400 adult blue butterflies, which together subsequently were handled another several hundred times. The stated objectives of the study were "to 1) determine the present distribution and population numbers of Smith's blue, at Marina State Beach; 2) determine which habitat areas of the dunes are important for mate location, foraging, and larval development; 3) evaluate different census methods for their appropriateness in future monitoring of Smith's blue during and after implementation of the revegetation program; and 4) provide management recommendations for Smith's blue at Marina State Beach."

As discussed above, the first and second goals largely could be met by simple survey and transect procedures, without handling butterflies. To use the most fragile, federally protected butterfly species as a lepidopteran guinea pig in pursuit of the third goal defies any sense of logic or conscience. Certainly a non-endangered, taxonomically related species could have been used to develop a low impact protocol for application to an endangered species. The fourth goal underscores the lack of pertinence of most mark-recapture studies to habitat management. The key recommendations stated at the conclusion of the study were "to control, and where feasible, eradicate alien flora that can outcompete native vegetation such as the butterfly's buckwheat foodplants" and to "promote natural dune dynamics, which facilitates natural seeding establishment by the native flora." Not only were those recommendations obvious from a cursory view of dunes blanketed with South African iceplant, but just such a restoration project was already in process. In other words, hundreds of endangered butterflies were subjected to physical impairment and potential mortality associated with handling for no good reason.

All this does not mean that no value whatsoever can be derived from mark-recapture studies of endangered butterfly species. Interha-

bitat dispersal can be crucial to the overall persistence of butterflies where adjacent populations exist or empty (but suitable) habitat patches are available. Gall (1984), for instance, used mark-recapture to demonstrate age-dependent dispersal in female *Boloria acrocnema* in an isolated Rocky Mountain habitat patch. He speculated that late season female dispersal may contribute to the colonization of new habitat patches. But one must ask whether similar insights into the population dynamics of species less physically hardy than *Boloria acrocnema* warrant the potential damage from intensive handling. I contend that they do not.

This paper is presented as a plea to government agencies, environmental consultants, and field biologists to restrict mark-recapture studies to non-endangered species, or to endangered species proven hardy enough to withstand human handling. In the latter circumstances, mark-recapture should be employed only to answer specific questions crucial to recovery strategies. The use of untrained field workers in such studies should be strongly discouraged. The preponderance of evidence indicates that the handling of lycaenid butterflies, in particular, usually results in the taking of individuals—an unlawful act under most permits to handle endangered species and one which should not be encouraged in the name of conservation.

It seems the ultimate irony that recent attempts at conserving our butterflies often have amounted to studying them to death.

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Opinion.

Reply to Scott's Criticism

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Differences of interpretation amongst authors dealing with the same set of facts are only to be expected in the literature of phylogenetics. However, when an author's work receives heavy refutation on grounds which (a) grossly misrepresent his own viewpoint, and (b) lean heavily on wrongful statements *of* fact, then it is necessary and right that these misrepresentations be exposed. The paper by Scott (1986) in this journal is the subject of the following commentary.

The following notes on the distribution of character states of Ditrysian Lepidoptera show that Scott's factual evidence runs contrary to established knowledge.:

Larval Characters:

(1) The loss of L3 on the prothorax is not restricted to Pyraloidea and 'Macrolepidoptera' — it is also found in the Scardiinae (Tineidae), Zygaenoidea, Epermeniidae and Glyphipterigidae-*sensu* Brock. Scott gives no explanatory comment on his placing of Carposinidae in Pyraloidea — and his placing of Mimallonidae in that superfamily runs contrary to characteristics of adult and pupa, his observations on larval morphology having been known since the work of Fracker (1915). In addition, some Pyraloidea (*sensu* Scott) actually *possess* the 'missing' L seta (Forbes, 1923). (2) Scott offers no reason for assuming that the Pyraloid 'L' group is *primitively* unisetose on abdominal segment nine. It is *often* bi- (sometimes tri-) setose in that superfamily. Again, the supposed absence of two of the three 'L' setae on the same segment for 'Macrolepidoptera' is in opposition to the presence of two 'L' setae on segment nine in Notodontidae and Drepanidae (Hassenfuss, 1969). The same reduction trend is seen in many members of the Tineoid complex (MacKay, 1972). (3) Scott is correct in stating that all 'Macros' have L1 and L2 separate on the abdomen. However, these setae are also dissociated in the (extralimital) Immidae (Common, 1979), and in monotrysian Heteroneura, Tineoidea *s. str.* (excluding Psychidae) and

Yponomeutoidea-*sensu* Brock. Other correlations of chaetotaxy could be taken to show that the 'Macros' evolved from Cossoidea. The condition of the 'L' setae in Mimallonidae (see above) could equally well serve as evidence that these setae were associated in the 'Macro' ancestor — as indeed suggested by Forbes. These 'wide-gap' character states occur separately in different families of Tineoidea *sensu stricto*. (4) The presence of secondary setae cannot be taken as a shared-derived trait of 'Bombycoidea-Sphingoidea-Hesperioidea-Papilionoidea'. Similar secondary vestiture is found in the (extralimital) Zygaenidae — and it is certainly *not* 'absent in Noctuoidea' as claimed by Scott (cf. Arctiidae, Ctenuchidae, Notodontidae, Acronictinae, etc.!). (5) Reduction of crochets from circlet to mesoseries is found within many ditrysian superfamilies, and the 'butterfly triserial condition' is found in some Cossoidea and Pyraloidea — even in groups as remote as Gelechioidea (Forbes, 1923). Intermediate stages are found in Geometroidea, as well as in Rhopalocera (amongst 'Macrolepidoptera').

Pupal Characters:

All characters of the 'Macrolepidopterous' pupa are found also in the 'Micro' groups Yponomeutoidea and Gelechioidea — while Scott's ancestor for Pyraloidea-Macrolepidoptera is clearly an incompletely obtect pupa. 'Spinose-protruded' pupae also occur in some Bombycoidea and Forbes (1923) records pupal protrusion for certain Pyraloidea. Some Psychidae have 'incomplete' male pupae, and obtect females!

Looking in greater detail at Scott's listing of pupal characters, it must be stated that: (1) Maxillary palpi are not 'lost' in 'Macros' — as stated by Mosher (1916) they are developed externally in many Noctuidae. (2) In placing Sphingidae in his Hesperioid-Papilionoid lineage, Scott cites 'loss of cocoon' as a shared derived trait — yet some Sphingidae are cocoon-builders. (3) Contrary to Scott's claim, neither Zygaenoidea nor Sesioidea have two rows of spines per segment. The primitive condition is one row for Zygaenidae, the spination becoming more diffuse in advanced forms. In Sesioidea, there is a single row per segment in Choreutidae — double rows only in Sesiidae and Brachodidae (Heppner and Duckworth, 1981). Similarly, the Tineoid superfamilies do not 'generally have one row...'; in this group, the Yponomeutoidea and Gelechioidea are never spinose/protruded — excluding genera of Tortricoid-Sesioid-Zygaenoid relationships wrongly placed in Yponomeutoidea by Common (1970) — see Brock, (1967, 1971), Heppner and Duckworth (*loc. cit.* above), Heppner (1977) and Kyrki (1984). Lyonetiid pupae are also non-spinose, and *two* spine rows have apparently evolved independently in some members of the families Psychidae and Gracillariidae (Mosher, 1916). (4) Mandible remnants are *not* 'definite bumps in Cossoidea-Castnioidea, weakly developed in butterflies'; the 'Cossoid-Castnioid condition' is widespread amongst 'moths' and the (non-

unique) 'butterfly condition', far from being weakly developed, involves an *enlargement* of these structures — so that right and left 'mandible remnants' almost meet along the median line (Mosher, 1916). In the same way, development of the clypeo-labral suture is variable in Ditrysia, and cannot be used as a 'shared-derived trait'. (5) Having used the presence of fore leg femur in the pupae of 'nearly all moths' (cf: 'shared-derived traits for monophyly of Hesperioidea-Papilionoidea'), Scott goes on to list the *exclusive* presence of the same trait as evidence for primitiveness of Geometroidea and Noctuoidea within his Macrolepidoptera. Loss of a visible fore-leg femur is also quite widespread amongst Microlepidoptera (Mosher, 1916). (6) Scott uses the presence of an epicranial suture/cleavage line as a further indicator of the primitive position of Geometroidea-Noctuoidea within 'Macros', yet fails to state the presence of this trait in some Bombycoidea; his substitution of *temporal* for 'epicranial' is based on an unlikely pupal-imaginal homology (Scott, 1985), and his statement (*loc. cit.*, and in the present diatribe) that the epicranial cleavage line is absent in Lycaenidae (contrary to Mosher) is incorrect.

Adult Characters:

   (1) Vestigiation of the Cup vein in the forewing is widespread amongst lower ditrysians (including some Cossoidea-Zygaenoidea), and in any case this vein is well developed in certain Bombycoidea. It cannot therefore be a 'shared-derived trait' of Macrolepidoptera. (2) Sharplin's summary of character states associated with the wing base in Lepidoptera (Sharplin, 1964) clearly states that Cossoidea, Castnioidea and Zygaenoidea either exhibit intermediate conditions between primitive and advanced Ditrysia, or else they carry advanced ('Macro') character states. Scott's manipulation of the Sharplin data requires support from described morphological observations — together with some indication as to how Sharplin herself came to be misled. (3) The 'discrimen' (mesal lamella) of the mesothorax shows variable development in Ditrysia, and its strengthening in 'Macros' is not an exclusive (or universal) attribute of these superfamilies (Brock, 1971). (4) The looped heart of 'Macrolepidoptera' is also developed in many Cossidae and Limacodidae — although not in Pyraloidea. Scott also states that 'moths' other than some Cossidae 'lack a chambered heart', following Hessel (1969), while the latter author states quite clearly (*loc. cit.*) that most 'Macro-moths' *do* have a chambered heart. Hessel's distinction between the groups cited by Scott was not dependent upon *presence/absence* of the heart chamber — but on *transverse versus horizontal orientation of the chamber itself.* (5) Scott presents no evidence whatsoever for his assertion that the Bombycoidea-Sphingoidea evolved from a tympanum-bearing ancestor. According to his scheme, the abdominal tympanum of Pyraloidea was ancestral to that of Geometroidea and Noctuoidea — yet

many Pyraloidea and Geometroidea lack a tympanum, and there is no definite evidence that this is a secondary development in either case. There is also evidence to suggest that the Noctuoid tympanum evolved *in situ* (i.e., on the thorax), rather than being a later advance on an originally abdominal tympanum. (6) The presence/absence of ocelli, chaetosemata and haustellum in Ditrysia follows such a widespread pattern of correlation in the taxonomic hierarchy, that no importance can be attached to this, above the level of family (Brock, 1971). (7) The loss of the upper sector of the precoxal suture/sulcus cannot be brought forward as a shared-derived trait for Bombycoidea-Sphingoidea-Rhopalocera. As stated by Brock (1971), this trend is widespread in other ditrysian superfamilies in which the suture is sometimes retained. Scott's treatment of this suture also implies two misidentifications in Brock (*loc. cit.*) — firstly, in his use of quotation marks: 'precoxal suture' of Brock; in fact, the term *paracoxal is nothing more than a doubtfully necessary replacement term of Matsuda (1970) for the widely used precoxal.* Secondly, Scott states (here, and in Scott, 1985) that the structure identified as 'precoxal suture' by me for Hesperiidae, is in fact the secondary sternopleural suture (a term originated by me to replace a misnamed suture of Ehrlich, 1958, still misapplied by Kristensen, 1976). If a secondary sternopleural suture does occur in Hesperiidae other than those I examined, then (a) Scott must name and figure examples, and (b) we require a more acceptable explanation from Scott as to why the precoxal suture vestige figured by me is 'misidentified'. (8) The distal enlargement of the antenna reported by Scott for Sphingidae (as a shared derived trait with Rhopalocera) is absent in *many* Sphingids (and present in many diurnal moths — e.g.: Agaristinae, Castniidae, Zygaenidae, Callidulidae, etc.). Its presence is clearly correlated with diurnal activity. (9) The 'areole' of the forewing radial system does not 'occur in most moths' — it is limited to a few families of Noctuoidea and Geometroidea and one of Bombycoidea, amongst 'Macros'. It is unlikely that true homology exists between the 'areoles' of these groups, or between any one of them and the (similarly sparsely distributed) 'areole' of lower Ditrysia (Brock, 1971). (10) The R4/5 branching basad of R1 in the radial system of Rhopaloceran pupae is found also in adult Castni-idae (see Forbes, 1923). Published sources of data on pupal tracheation of 'moth' groups are too fragmentary to allow broad generalisations to be made at this stage. (11) Fusion of the anapleural cleft, listed as a shared-derived trait for Hesperioidea-Papilionoidea by Scott (contrary to Kristensen, 1976 — following Brock, 1971) is a feature of some diurnal 'moths' (and in any case, is not apparent in Hesperiids). (12) 'Mesal fusion of the metathoracic furcal arms' is also listed as a shared derived trait of Hesperioidea-Papilionoidea by Scott, but this occurs also in Pyralidae (although not in other Pyraloidea — see Brock, 1971). Scott also erroneously refers to fusion of furcal *arms* — whereas it is the *dorsal laminae* of these structures which form the fusion (this same

character is listed by Kristensen, 1976 as a 'probable synapomorphy' of the same group). (13) The reduction of sternal apodemes (of abdominal sternite two) in Rhopalocera is a widespread trait in Ditrysia — including Limacodidae, Saturniidae, Thyrididae, and of course, many tympanum-bearing families (Brock, 1971). (14) Scott mentions similarities between Hesperiidae and 'Macro-moths' in compound eye structure. Following Yagi and Koyama (1963), this correlation lies with the more primitive Bombycoidea *alone* — although these workers report a similar correlation with the 'non-Macro' *Cossidae* — a fact not mentioned by Scott. The same authors found a natural lineage between the compound eye conditions of Pyraloidea-Geometroidea-Noctuoidea, this apparently unconnected with the Cossoid/Hesperioid/lower Bombycoid eye — although many convergencies were evident between diurnally active members of quite remote families. These broader findings are entirely ignored by Scott. In the lack of any good functional explanation of the data on the compound eye, we do not know how (or *if*) the Cossid condition could form a transition to that of the supposed Pyraloid lineage — although its (theoretical) connections with Hesperioidea and Bombycoidea are clear enough. (15) Scott lists the reduced condition of the maxillary palpi in 'Macrolepidoptera' as diagnostic, yet three-segmented palpi are reported for Carthaeidae of Bombycoidea by Common (1966, cited in Brock, 1971). Reduction of palpi is found in many 'Microlepidoptera', including Cossoidea, Zygaenoidea, and even Tineoidea (Psychidae).

Given the high degree of polyphyly in the characters listed, it is not possible to use them either as diagnostic features of suprafamilial groups — or as monophyletic character changes along the branches of Scott's phyletic tree. Many provide useful suprageneric characters, but all are known to be unstable at higher levels. Scott also uses *primitive* character states as indicators of affinity (as indeed in his parallel paper on butterfly phylogeny, Scott 1985). This 'phenetic' approach is universally rejected by all cladists. In the same way, Scott's use of 'secondary loss' characters cannot have much relevance to phylogeny reconstruction.

Scott's attack on certain phyletic relationships suggested by me completely overlooks the *indirect ancestor concept* (see Cracraft, 1974), yet this too is regarded as a fundamental principle by phylogenetic systematists. *No* direct ancestor relationship was ever proposed by me, for any ditrysian superfamily pair — and to argue against theories of *indirect* relationship on these grounds is nothing more than the knocking-down of a 'straw man' hypothesis.

Scott's table of characters actually shows 'plus-minus' entries (providing 'modified weighting') for some characters listed in the accompanying text as either 'plus' or 'minus' for the same taxa. An expansion of this table to incorporate all other characters (and all other Ditrysian superfamilies — with many more 'pluses' and 'minuses' corrected to

'plus-minus') would agree pretty well with the general conclusions of Brock (1971) regarding the lability of the vast majority of characters available for higher classification and phylogeny reconstruction at superfamily level and above in Ditrysia.

Looking more deeply into the question of misrepresentation of my own views — I find no mention whatsoever of the fact that my 'selection of characters' was empirically based (*loc. cit.*, p. 30). My final analysis was stated, character-by-character, at some length — far from being the 'intuitive' system Scott claims it to have been. That analysis was placed firmly in perspective with the broadest conclusions of the classical authors working with the early stages, with actual quotations from the contributions of Hinton (1952) and Chapman (1896) incorporated in the text. In the same way, the broader conclusions of Yagi and Koyama (1963) and of Hessel (1969) are either ignored or misrepresented by Scott.

Based on the widespread manifestation of polyphyletic trends at and above superfamily level in Ditrysia, I had argued that an explanation could be found in the phenomenon of gradistic evolution (following the terminology of Huxley; cf. Huxley, 1942/63) — and that the higher groups Macrolepidoptera and Microlepidoptera were in fact, gradistic constructs — this hypothesis being based on three main facts: (1) the diagnostic traits of 'Macro' grade had virtually all evolved in several 'Micro' superfamilies, (2) the majority of 'Micro' grade characters are to be seen distributed amongst primitive members of the 'Macro' super-families, and (3) most of these trend characters seemed correlated with the change-over from endophagous to exophagous larval habits. This is not the place to go into this hypothesis is detail, but Scott omits all reference to this central theme of my earlier paper. Subsidiary to that thesis, was an arguable hypothesis for cladistic relationships between members of 'Macro' and 'Micro' grade, based upon those trends which seemed the least labile. The gradistic concept of large-scale evolu-tionary change presents an obstacle to those cladists who are certain that phylogeny can always be worked out on the basis of 'synapomorphy' and gradism has the further 'wrong' attribute of being highly 'non-parsimonious'. Whichever way we look at the data for Ditrysia, there are virtually *no* 'synapomorphies' for units above superfamily — with many superfamilies themselves based on polythetic distribution of character states for included families. Basic to the question of gradistic evolution is the related typological problem of 'wide phenetic gaps' between 'Micro' and 'Macro' superfamilies. For example, arguments concerning the possibility of an indirect ancestry relationship between Castnioidea and Rhopalocera invariably cite 'Micro' grade features of Castnioidea (many of them lost in advanced Castniids!) as evidence of 'unbridgeable gaps' between these taxa. The strongest of these 'gap' character complexes lie with the larval and pupal stages — yet no one objects to similar 'gaps' existing within families which display both

endo- and exophagous biology (e.g., Pterophoridae, see Brock, 1971). Secondly, the same authors seem unconcerned by the presence of 'incomplete' and obtect pupae within single families like Yponomeutidae (*sensu* Common) and the Lyonetiidae of many recent authors. Either these features are indicative of 'unbridgeable gaps' (equals Special Creation?) or else they are potentially rapid adaptations (as suggested by their taxonomic correlations).

The exceedingly widespread expression of parallelism at higher levels in Ditrysia surely points to a major feature of the evolutionary process itself, rather than an attempt by Brock to upset the theories of some cladists and pheneticists. The way forward from this point must surely be to look more deeply into the morphology of the lower Ditrysia, and to re-examine larval and pupal morphology — looking for functional explanations in these data — along with that presented by Yagi and Koyama on the compound eye and by Hessel on the aorta and associated structures. Anything less stands in grave danger of being categorised as what H.E. Hinton once described as 'a kind of juggling with the facts — by persons with limited direct knowledge *of* the facts'. Granted, there *are* alternative theories to the one I proposed — but we require better representation both of existing knowledge *and* of other proposed theories, than that now put forward by Scott. Impediments to such progress are numerous — many families of Ditrysia are poorly represented in collections and often early stages are little known — even undiscovered. Functional explanations of morphological trends are often evasive. Some authorities in a position to help with certain of these problems are actually hostile to the continuation of work of this kind — many lepidopterists will only support work in 'safe areas' which pose no apparent threat to established classifications — 'the stability of Lepidoptera classifications since Herrich-Schaeffer' having been one 'justification' for a personal attack on my work by an 'authority' at the British Museum in London, which probably did more than anything to impede further progress.

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Notes

Notes on the biology of *Brephidium exilis* (Boisduval) (Lycaenidae)

Brephidium exilis (Boisduval) is a common butterfly throughout much of the western United States, where its distribution stretches as far north as Oregon. Since Edwards (1894, Can. Ent. 26: 37−38), several authors (Coolidge, 1924, Ent. News 35: 115−121; Shapiro, 1972, J. Lepid. Soc. 27(2): 157−158 and Johnson, 1984, J. Res. Lepid. 23: 104−106) offers data concerning aspects related to its host plant and behavior.

In September and October of 1985 I studied some aspects of the biology of this species on the U. C. Davis campus. Around Davis, Yolo Co., California, *B. exilis* forms populations considered colonizing or fugitive (Shapiro, 1980, Atala 8(2): 46−49). In this locality I have seen this species often flying around *Bassia hyssopifolia* (Pallas) Volk., *Suaeda fruticosa* (L.) Forsk, *Atriplex argentea* Nutt. ssp, *expansa* (Wats) Hall & Clem. and *Salsola australis* R. Br. (all Chenopodiaceae) and *Amaranthus graecizans* L. (Amaranthaceae). In this paper some aspects of the biology of this species in a colony which was flying around *S. australis* and *A. graecizans* are described. Both plants were growing on waste ground. *S. australis* grew in a semispherical fashion, reaching a height of about 1 m with some 60 individual plants spread over a distance of 100 m between the two furthest apart. *A. graecizans*, on the other hand, is a creeping plant. In the study area its distribution and abundance are similar to the latter. Both are annual and reach maximum development during late summer and early autumn.

In September, *S. australis* is in full flower. *B. exilis* flies preferentially around the bushes of this species, upon which courting, mating and egglaying are carried out. The light bluish-green eggs are laid near the flowers of *S. australis*. For this purpose the female walks up and down the branches and after trying out different flowers, lays just one egg close to one of them, flying off then to search for another place to lay the next egg. Oviposition occurs also on *A. graecizans*, although egglaying on this foodplant is less frequent.

In spite of their abundance, the caterpillars are difficult to find on the food plant. On *S. australis* they feed on the flowers introducing the forepart of their body into the axils of the bracteol which supports the flower. The *B. exilis* caterpillars frequently attract ants. *Conomyrma insana* Buckley (Formicidae: Dolychoderinae) is often found around them and occasionally several specimens around the same caterpillar. Due to the crypsis of the caterpillars on the food plant, the best way to locate them is to follow the ants which attend them. *C. insana* may play an important role in protecting the caterpillars from fly parasitization. It has been observed that when a larva is approached by the fly *Aplomia theclarum* Scudder (Tachinidae), attendant ants become very agitated, forcing the tachinid to fly off again. Similar bahavior has been reported by Coolidge (1924, loc. cit.). Nevertheless a large number of caterpillars collected in the field and reared in the laboratory contained the parasitoid larva, which emerges in the last larval instar. The fly's pupal stadium lasts about 12 days.

With the first autumn rainfalls the population of *B. exilis* decreases rapidly. According to Coolidge (1924, loc. cit.) hibernation takes place as pupa. Shapiro

(pers. comm.) states that no live pupa have been found near Davis after Christmas, and that the species resumes flight in late Spring (April to June in different years), suggesting annual reimmigration.

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Courtship of a model (*Adelpha*; Nymphalidae) by its probable Batesian mimic (*Limenitis*; Nymphalidae)

Silberglied (1977, in *How Animals Communicate*, T. Sebeok, ed., Indiana Univ. Press, Bloomington, Indiana) suggested that optimal mating behaviors of organisms involved in mimicry associations should involve communication modes not shared by vertebrate predators. Because predation pressure causes natural selection for convergence in flight behaviors as well as gross wing pattern characteristics between mimics and their models, behaviors associated with species recognition during courtship are expected to not rely heavily on visual cues whether the species involved is a model or a mimic.

Observations on interspecific courtships allow insights concerning which traits are important for mate recognition within species. Shapiro (1985, J. Res. Lep. 24: 79−80) reported a case of confounded courtship where in the male of a presumed model species (*Erynnis propertius* Scud. & Burg., Hesperiidae) pursued a female mimic (*Euclidea ardita* Franc.; Noctuidae). Contrary to the prediction above, the male appeared to be relying exclusively on visual cues. In the following case the sexes are reversed − the pursuing male is the mimic.

Adelpha bredowii californica (Butler) and its presumed Batesian mimic *Limenitis (Basilarchia) lorquini lorquini* (Boisduval) are sympatric below 2100 m. elevation throughout the Coast Ranges and Sierra Nevada in California. Both species are dark brown with a prominent creamy white band across both sets of wings and an orange tip on the forewing. These butterflies fly together in the same canyons, and males often compete for territories in the sunny patches of stream beds. The mimicry relationship has never been formally tested, but is widely inferred from both the sympatry and the documentation of Batesian mimicry in other species of *Limenitis* (e.g., Platt, Coppinger, & Brower, 1971, Evolution 25: 692−710).

While collecting *L. lorquini* and *A. b. californica* for laboratory studies, I encountered a male *lorquini* courting a female *b. californica*. The sighting occurred at 1355 hrs, 22 April 1986, in Mix Canyon, Solano Co., California (approx. 10 km. north of Vacaville), and lasted until 1359 hrs, when the pair was lost from sight. When initially encountered, the courtship was in progress, with both butterflies fluttering one to two meters above the road at the edge of a small sunlit area. After about thirty seconds, the female began flying faster,

with the *lorquini* in hot pursuit (i.e., within 10 cm). The pair made a number of wide circles in a large (30 m) sunny area above a stream adjacent to the road, ending when the female alit on a shrub (*Quercus dumosa* Nutt., Fagaceae; a possible foodplant of *b. californica*). The *lorquini* male immediately alit beside her and nudged her with his curled abdomen in repeated attempts to copulate. The female avoided this by turning her abdomen away from the male or by short flicks of the wings. These behaviors continued for approximately one minute, then the male flew to a nearby (2 m) bush and perched while the female basked. When the female flew again after an interval of approximately 90 seconds, the male gave chase, and the pair was lost from sight. The weather was sunny and clear with little wind, temperature approximately 26°C. *A. b. californica* males were quite common in the canyon, but only eight *lorquini* males were seen over the span of three hours. Additionally, three *b. californica* females and one *lorquini* female were collected. These densities are representative of most spring seasons.

Because I did not see the beginning of the encounter, it is not clear whether the female above initiated the fluttering courtship flight using wing pattern cues from the male *Limenitis*, or if receptive females simply initiate the fluttering flight whenever pursued. It does appear clear, however, that the female *Adelpha* rejected the inappropriate suitor only after she had begun the fluttering courtship display. Whether this was on the basis of visual or pheromonal cues remains unknown. The male *lorquini* seemed completely unaware of his *faux pas* throughout the encounter. As in *Erynnis* reported by Shapiro (*op. cit.*), male *Limenitis* appear to rely exclusively on visual cues during courtship.

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A Bibliography of *Euphydryas*

Checkerspot butterflies of the genus *Euphydryas* are among the most well studied Lepidoptera, and have become key organisms for testing ecological and evolutionary theory. Here we have compiled a bibliography of papers concerning this genus. We suspect that this bibliography will be a useful resource both to those working directly with *Euphydryas* and to those with a more general interest in butterfly ecology. The topics included cover distributional notes, population dynamics, population genetics, host plant and parasitoid interactions, and behavior. We have endeavored to make this bibliography as complete as possible, but in an effort to produce a bibliography of manageable size we have excluded most taxonomic descriptions. Those for the most part are referenced in Gunder (1929), Miller and Brown (1981, A Catalogue/Checklist of the Butterflies of America North of Mexico. The Lepidopterists Society Memoir No. 2), Kudrna (1985, Butterflies of Europe; Concise Bibliography of European Butterflies. AULA-Verlag Wiesbaden), and various works by Higgins.

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Aberrant Polyommatinae (Lycaenidae) from Ohio and Florida

Aberrant Polyommatinae have recently been illustraded by Wright (1979, J. Lepid Soc. 33: 266) and Neil (1983, J. Lepid. Soc. 37: 258). Presented here are three extreme aberrations in pattern not previously recorded.

On 19 April 1986, at Shade River State Forest, Meigs Co., Ohio, an aberrant female *Glaucopsyche lygdamus lygdamus* (Doubleday) was collected in a rich stream valley near Forked Run State Park. The individual was found in

association with wood vetch, *Vicia caroliniana* Walt., which grows abundantly along a SE-facing roadbank. This plant is the primary hostplant of the species in Ohio. Between 1030 h and 1200 h the author and D. C. Iftner collected and observed several *G. lygdamus* flying in the vicinity of wood vetch and visiting damp soil along a dirt township road that traverses the valley.

The aberrant female (Fig. 1b) is striking in that the normal basal and postmedian black spots on the ventral surfaces of the hindwings are totally lacking. The small discal bars are the only remnants of normal maculation. The postmedian row of spots on the ventral surface of each forewong is dis-placed inwardly and is found just beyond the cell. The ventral surface of the left forewing possesses five spots while the opposite wing exhibits only four. The dorsal surfaces are normal. Although *G. lygdamus* is highly variable both individually and geographically, this aberration illustrates a phenotype never before observed in Ohio.

Two aberrant individuals of the subspecies *Hemiargus thomasi bethunebakeri* W. P. Comstock and *Hemiargus ceraunus antibubastus* Hubner were captured in extreme southern Florida. The former specimen (Fig. 1d) is a worn male taken 14 December 1982 on Key Largo, Monroe Co. Ventrally, the forewings possess enlarged and lengthened white areas that taper basally. The hindwings lack the black portions of the basal and costal spots. The postdiscal white band is expanded and tapers inwardly.

The individial of *H. c. antibubastus* (Fig. 1f) is a male in good condition taken 1 September 1982 on Stock Island, Monroe Co., Florida. The specimen has a grossly atypical pattern ventrally. The wing surfaces are almost completely suffused with white scales, creating a submarginal band of dark spots on the forewings. The hindwings slightly differ individually. The two black costal spots of the right hindwing are enlarged and the outermost spot appears "smeared". Two dark postdiscal bands extend completely across the wing. The left hindwing

Fig. 1.   Aberrant and normal specimens of three species of Polyommatinae a. Normal male *G. lygdamus*, b. Aberrant female *G. lygdamus*, c. Normal male *H. thomasi*, d. Aberrant male *H. thomasi*, e. Normal male *H. ceraunus*, f. Aberrant male *H. ceraunus*.

lacks the innermost black costal spot but a "smeared" outermost spot is present. A dark postdiscal band extends across the wing and a partial second band extends from the inner margin to CU_1.

The specimens figured are in the collection of the author.

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Ommochromes in Libytheidae

Ommochromes are a group of pigments that occur as granules in insect eyes and in various other organs and tissues (Robinson, 1971, Lepidoptera Genetics, Pergamon Press, Oxford). The red meconium of teneral adults, which contains ommochromes, is widespread in Pierinae and Nymphalinae and is also known to occur in a few Coliadinae, *Charaxes*, and certain Parnassiinae (Shapiro, 1982, J. Res. Lepid. 20: 97–102). Some Pierinae have red eggs which may be a manifestation of ommochromes (Shapiro, op. cit.); ommochromes can also be brown in color (Robinson, op. cit.). Since pterins and ommochromes are often associated in insect eyes (including Lepidoptera) and tend to be affected by the same mutation, it is thought that certain pterins are involved in the enzymatic processes that form ommochromes (Robinson, op. cit.; Gilmour, 1961, The Biochemistry of Insects, Academic Press, New York & London). It was recently discovered that some Libytheidae contain pterin pigments in their wings (Shields, 1987, J. Chem. Ecol., in press).

The meconium of two freshly emerged *Libytheana bachmanii bachmanii* Kirtland from College Station, Texas, was light reddish orange to moderate orange with brown speckles, i.e. rust tan or testaceous in color (T. Friedlander, in litt.). When this species is ready to pupate, it spins a button of red silk on the underside of a leaf (Edwards, 1881, Canad. Ent. 13: 226–229). When first laid, the egg of *Libythea laius* Trimen is whitish but in two days turns to a pale, dull salmon tint; similarly, *Libythea celtis celtis* Fuessly eggs turn brownish-pink (Shields, 1985, Tokurana 9: 1–58). These data suggest the Libytheidae may also contain ommochromes.

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Book Reviews

THE BUTTERFLIES OF NORTH AMERICA — A NATURAL HISTORY AND FIELD GUIDE. Scott, James A., Stanford University Press, Stanford, California. 583 pages, hardback. $49.50.

This is the new definitive treatment of North American butterflies and skippers. It replaces the book edited by W. H. Howe that was published in 1974. Howe's book appeared 44 years after the previous compendium by W. H. Holland. The reader may ask 'Is it really necessary to have another new butterfly book so soon after Howe's treatment?' or 'How does Scott's book compare with previous books?'

Howe's book was really written in the late 1960's but took more than 5 years in the production process so the span is a bit more than mere subtraction of years would suggest. Scott attempted to keep his text as current as possible up to about a year before actual publication. Twenty-one authors contributed to the Howe book and the text was edited by F. M. Brown and H. K. Clench. In contrast, the entire text of the new book was written by a single author — a monumental undertaking. The two books differ in many other ways as well. The Howe book is illustrated with 97 plates with beautiful color paintings by the editor, whereas the new work includes 64 color plates of photographs of butterfly specimens and shots of living individuals. I consider Howe's plates superior, although many species not found in the Howe book are newly illustrated by Scott. The larger and lighter butterflies are best shown by Scott's photographic plates, but the smaller darker butterflies — often too many on a single plate — lack sufficient contrast to be shown well. In addition, most of the specimens are from Scott's own collection, and the ventral views show the ravages on the butterflies of having died between thumb and forefinger, i.e. missing legs and vestiture.

Scott's book places a much greater emphasis on behavior, host plants, and ecology than any previous North America-wide treatment. The book has 153 pages of introductory chapters, followed by 348 pages of species treatments, and ending with 45 pages of appendices.

The introductory chapters are almost like a separate book on butterfly evolution, structure, and biology. This reviewer is amazed at the amount of technical material included. Many readers will find the introductory sections like an introductory text in its content, but will find many of the technical terms softened by the author. I found a few bothersome, e.g. 'jaws' instead of 'mandibles,' and 'blood' instead of 'hemolymph,' but most readers will not mind. Scott also uses mechanomorphisms such as tracheae being 'constructed like vacuum cleaner hose.' Most of the material is accurate and factual, but there are some inaccuracies such as the statement on p. 42 that 'butterflies only fly when the sun shines' and that on p. 26 that implies females of all or most species are larger than their males. Anyone who has observed butterflies in eastern North America can vouch that many species fly in numbers on cloudy days. Likewise, males of many pierid species are larger than the females, and most lycaenids have no significant size difference between the sexes. It is difficult to ascertain which information is the result of Scott's research, which is opinion, and which has been taken from other works. In some cases literature sources are referred to by the author's last name and first initial, but no indication of the literature citation is to be found later in the book, in other cases this reviewer found

instances of results from works other than Scott's given with no attribution. In a similar vein some of the line illustrations that appear throughout the book, mostly drawn by Scott, are taken directly from the works of others without acknowledgement. Much of the introductory material will prepare the reader for the species treatments that follow, e.g. chapters on behavior, reproduction, migration, and geographic variation, but others are of no use later on. Examples of these are the excellent keys to first instar and mature larvae, pupae, and adults, but on page 158 the reader is told "To identify an adult butterfly, first compare the butterfly you have found with the butterflies illustrated on the color plates, and settle on its probable identity." Why, one wonders, were the keys included?

The species treatments will be the 'meat' for most lepidopterists, and I will devote most attention to them. First it is worth comparing the taxa included with those in the 1981 Miller and Brown Catalogue/Checklist (Lepid. Soc. Mem. No. 2). At the suprageneric level Scott follows the Ehrlich classification — recognizing five families of Papilionoidea (Papilionidae, Pieridae, Lycaenidae, Libytheidae, and Nymphalidae) and one of Hesperioidea (Hesperiidae); while, in contrast, Miller and Brown split the Nymphalidae into 5 separate families while recognizing the others. At the subfamily level the splitting approach is further executed by Miller and Brown as they recognize several subfamilies that in the eyes of this reviewer are placed at least one level too high, i.e. Argynninae, Melitaeinae, Marpesiinae, Charaxinae, Apaturinae. Scott's subfamily treatment is suitably conservative, fitting well with those for other Lepidoptera Superfamilies. Scott's apparent recognition of the unnatural higher groups 'Macrolepidoptera' and 'Rhopalocera' in his only black mark in the higher classification discussion.

At the generic level the contrast between Scott versus Miller and Brown continues. Miller and Brown raised subgenera and some species group names to genera, and considered North American butterflies to belong to 241 genera, while Scott, in a more conservative treatment, considered the same species to comprise only 203 genera, 38 fewer than the former work; 5 other genera in Scott's treatment are due to Hawaiian species(3) and Mexican species(2) newly reported in North America.

At the species level Miller and Brown listed 763 species, but felt that 14 were improperly reported; thus they attributed 749 species to the North American fauna. In contrast, Scott includes 679 species, but 6 of these are Hawaiian not included by Miller and Brown, 2 listed as probably not North American, and, finally, 17 are newly reported for North America: *Staphylus azteca, Arteurotia tractipennis, Autochton cincta, Amblyscirtes* unnamed (sic!), *Vettius fantasos, Synapte syraces, Piruna cingo, Callophrys herodotus, Boloria natazhati, Chlosyne marina, Precis genoveva, Epiphile adrasta, Oeneis alpina, Erebia occulta, E. kozhantshikovi, Phoebis orbis,* and *Papilio victorinus.* This makes the comparable species number for Scott's book 654 — 95 species fewer than Miller and Brown! What is the reason for this disparity? The answer seems to be splitting on the part of prior revisers reported by Miller and Brown and some lumping on the part of Scott. Examples of needless inclusions as full species in Miller and Brown are hybrids (*Colias boothii|hecla × nastes|* and *Anthocharis dammersi |sara × lanceolata|* as well as many members of closely related parapatric and allopatric species complexes, e.g. *Asterocampa, Coenonympha,* and

Agathymus. On the other hand, Scott eliminates many of these excesses, but probably goes too far in the other direction by lumping as conspecific good biological species. Some of these are each other's closest relatives, but Scott seems to use any evidence of hybridization in nature as cause for lumping. Unfortunately, the rationale for these actions is usually not given. In addition, some species are lumped under their closest Palaearctic relatives even though no biological studies to justify the actions have been reported. Some of these may make sense; examples are *Pontia occidentalis* under *Pontia callidice*, and *Euchloe ausonides* under *Euchloe ausonia*.

For 30 years or more, the trend in animal systematics has been to deemphasize subspecies. Examples are the current checklists for North American birds and mammals that exclude listing of any subspecies. Scott's book includes 430 subspecies above the given nomenotypic taxon for each species, whereas Miller and Brown list 745 subspecies above those necessitated by listing the species itself. This is a strong reduction of 315 names, and most of the missing names will leave no voids in any meaningful discussion of geographic variation. Yet, Scott does apply the criteria for which subspecies to include in his book very unevenly. Virtually all of the subspecies described by Scott himself are mentioned, but others that seem more significant are omitted or lumped.

Whether intentional or not, Scott's systematics is unorthodox. Some populations are mentioned as 'subspecies unnamed' — a meaningless designation, and, more importantly, the authors are given for none of the included scientific names. The reader is referred to the Miller and Brown treatment for authors' names and citations, yet many species not listed by those authors are given and many new combinations are presented.

Looking at the species discussions themselves one finds the real heart of the book, and there is little to fault. Under each species there are 4 paragraphs — one for identification features of the adults, one to describe habitat, geographic range, and larval host plants, one for a thumbnail sketch of the early stages, and one to describe voltinism and adult behavior. A small but accurate range map is included in the margin for most species. Scott's researchs have been nearly exhaustive and the pages devoted to the species treatments are absolutely packed with valuable information. This reviewer found that the given southern terminus of the range for many species extending into the Neotropics fell far short of the known southern limits; apparently Scott did not look at any collections or much literature on Neotropical butterfly ranges. Some examples are *Eurytides philolaus* — Scott gives south to Honduras, actually south to Costa Rica, and *Apodemia multiplaga* — Scott gives south to Puebla, Mexico, actually south to Costa Rica.

Some of the wording in the species treatments is a bit bothersome; for example butterflies do not 'sip mud,' but they may sip moisture from mud or wet sand.

The appendices are valuable. They contain lists of species from islands in the vicinty of North America — Iceland, Greenland, Bermuda, and Hawaii; and techniques for collecting and studying butterflies. Scott continues the 'pinching technique' for the dispatch of specimens, instead of the use of poison which does not cause the loss of legs or distortion of the body. The techniques described are valuable and usually expedient. Especially valuable are techniques for studying life stages and marking butterflies. Many of the line drawings used to illustrate the genitalia dissection technique paragraphs are borrowed from other works without attribution.

Ending up the book is a woefully inadequate bibliography (see above), an excellent 'hostplant catalogue' — but numbered cross references to butterfly names earlier in text reduce the value for quick reference, an excellent glossary for the nontechnical reader, and a long detailed index to general subjects and butterfly names.

It will probably be at least a decade before another North America-wide compendium appears. For the person interested in observing butterflies as a naturalist or for people interested in conservation, the book has minimal value. Despite its title the book is not one you would want to put in your back pocket for a hike and it does not cater to non-collectors. In summary, the book has a lot of positives and some detractions, but all butterfly collectors and biologists who study butterflies will want the book on their shelves.

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To judge from its self-congratulatory Preface, this most recent in the spate of books on North American butterflies represents *the* comprehensive treatise — superceding and subsuming the many regional treatments and few synthetic volumes to have appeared in the past several decades. It is indeed such a bid on an authoritative treatise, like Howe (1975) for the whole fauna, and Opler & Krizek (1984) for the eastern states. And although its title might imply so, it is neither a field guide (Pyle's several books are) nor really a natural history (Opler & Krizek's is of that genre, if anything can be).

Scott's book is among the lengthiest produced in recent years, bursting its seams with biological and taxonomic minutiae at every turn of the page. It therefore warrants an exhaustive review, so please bear with me. Since other opinions are always instructive, I've sprinkled in excerpts from Paul Opler's initial review of this book in the *Audubon Naturalist News* (Vol. 13(1): 6), Art Shapiro's in the *Journal of the Lepidopterists' Society* (Vol. 40(4):356-357), and Jeff Glassberg's in the *Mulberry Wing* (Vol. 2(4): 4-6).

1. Generalities

The prose is staccato. As a consequence, the book doesn't read as smoothly as it could, wanting still for further grammatical editing. Opler's review termed the text "concise, sparse, and direct."

The positive points of the book are at once identifiable. These include: (1) novel keys to the newly hatched and full-grown larvae, and pupae of North American butterflies; (2) much hostplant information, with copious attendant details; (3) exhuastive treatment of butterfly physiology and behavior; (4) a well-armed assault on the phyletics of Lepidoptera using largely morphological characters; and (5) basically sound, diagnostic photographs of the Nearctic taxa.

The size of the book and these novel sections thus produce a powerful, impressive first feel. But that's where the buck stops, because these good portions are permeated and surrounded by some really bad ones.

The most horrifying problem with the book is a nearly total absence of accountability throughout: (1) no proper references in the text to the original

scientific literature; (2) frequent failure and/or incompleteness in delimiting Scott's observations from those made by others, leading de facto to inappropriate attribution of much work; and (3) an insensitivity to providing such documentation for the reader's benefit and the scientific record, particularly for the many new claims that are made.

Well into the book, on page 22, one excavates the first attributed piece of information — "(J. Osborne)" — in regard to ligaments in the anal region of larvae. Such incomplete parenthetical teasers are all the reader is ever offered in the text of this book. Unfortunately, these are useless as reference fodder, since the reader hasn't the slightest clue as to whether they refer to published papers (proper attribution would be the usual "[whomever, year]"), letters to the author (proper attribution would be "[whomever, in litt.]"), or conversations or telephone calls (proper attribution would be "[whomever, pers. comm.]").

Glassberg's review put it only slightly differently: "It is usually impossible to know if some piece of information is 1) generally accepted as true by the scientific community, 2) controversial and based on the publications of another author, 3) based upon the published studies of the present author, or 4) based upon the unpublished studies or opinions of the present author. [Points] 2 and 3 are unfortunate in that the reader accepts information as 'true' although it is known to be controversial. [Point] 4, presenting information in a pseudo-authoritative textbook form when no published, preferably refereed data exist to support one's statements is akin to intellectual dishonesty." And Opler's review termed Scott's referencing "unconscienably brief," which clearly logs in as a glowing compliment.

What useable citations are provided for the reader, then? Scott's bibliography numbers a scant 25, of which 22 simply are other general works. That leaves 3 to cover the available original scientific literature on the North American lepidopteran fauna. Two of these prove to be papers by Scott; no references to hallmark papers in lepidopterology, and no references to solid technical research.

What a *ridiculous* false economy of attribution! Opler & Krizek's book cites 254 scholarly articles — a full order of magnitude more — for the eastern taxa alone. Ferris & Brown (1981) cite 143 for just the Rocky Mountain region species... and so forth. Never before have I read a comparably sized recent work on any insect group *that claims to be a standard in its field* make so many novel assertions that simply can't be traced. Even if one entirely ignores these matters of good science and ethics, a major referencing problem still remains — namely, that the budding lepidopterist receives not a hint on where to turn in the literature for further enlightenment.

In short, the lack of accountability renders the book essentially useless as an educational tool. Appropriately, most serious workers have already all but dismissed it in this context.

2. Biological & ecological considerations

Scott's training is in butterfly behavior and ecology. Part I (Biology and Ecology, pp. 9-118) of the book thus addresses his forte, and most of it is essentially accurate in detail, though unreferenced.

Of special value are the extended discussions of the immature stages. The larval keys, as noted earlier, are most welcome additions. Lacking is comparable treatment of the eggs, with no mention being made of the available

exhaustive Palearctic lepidopteran egg atlas by Doring (1955), and Hinton's (1981) vast scanning electron micrographic egg survey of all insects. Although *Immature Insects* (Stehr, 1987) is too recent to have been cited, it is a volume that the interested reader should consider browsing regardless.

The section "Evolution and the Fossil Record" (pp. 84-101) is chock full of potentially revolutionary information for the systematist, if he/she can manage to plow through it (here is where a few skillful tables would have saved much paper), and can obtain further details as to its origin.

Despite its basic solidity, Part I is punctuated with "just so" fables (affectionately dubbed "offhand, undocumented zingers" in Shapiro's review), many of which prove to be absurd biological errors. An exemplar is the repeated assertion that the V-shaped impressions of bird beaks not infrequently found on wild-collected specimens indicate that "butterflies often escape when the bird tries to swallow" (e.g., pp. 3, 70). Apparently, Scott doesn't often consult studies on *moth* biology published alongside those on butterflies in the *Journal of the Lepidopterists' Society*. Therein, the morphology of bird beak-marks — which represent voluntary releases on the part of the bird, for any of a variety of reasons — and escape-tears are rigorously categorized, and their genesis cleverly documented experimentally (e.g., Sargent, 1973, *J. Lepid. Soc.* 27:175-192, and his 1976 underwing treatise, *Legion of Night*; note also the many comparable studies on butterflies during the middle part of this century that Sargent cites).

Lastly, consider the foodplant compilations. They are exhaustive, they are largely accurate. But, on balance so have been the foodplant compilations in the other recent butterfly books. Moreover, Opler & Krizek also adequately delimit local versus regional preferences; Scott does not. Tietz (1971) gives us an encyclopedic array of literature references with which we can trace foodplant records as we wish; we can't do so with Scott's listings. Scott slaps Tietz's cheek several times and admonishes us to check "every reference" therein for errors, flagging these records in his species accounts with a T superscript. But Tietz (1971) never pretended to trap all or even most of the published errors — that work was offered as a bibliographic tool. It would have been much more valuable for Scott to have superscripted his *own* records in this book with an S, and to have assigned other appropriate superscripts to original literature references he considered valid, and to unpublished foodplant information contributed to him by other lepidopterists.

3. The geography of Nearctic butterflies

Scott's range maps often inappropriately fill in truly discontinous distributions. This is immediately clear in a number of instance with the eastern taxa (e.g., *Satyrium edwardsii* in the upper midwest, *Poanes massasoit* in the northeast, and *Mitoura hesseli* throughout its range), and a scan of the Opler & Krizek maps suggests the problem could be endemic throughout Scott's book. Compare, for example, Opler & Krizek's maps for other selected eastern skippers (map 223 p. 229, map 241 p. 243) with Scott's (bottom p. 440, top p. 450).

Of course, some discrepancies between these two books likely reflect advances in regional sampling since 1984, when Opler & Krizek's book came out. Other discrepancies may point to old records, and/or possibly document extinctions and range contractions over time, information of crucial importance. How would we tell? In the texts would be where to root around for clarification. Let's do so.

The range information provided by Scott for *Problema bulenta* (p. 450), for example, is so terse as to be misleading at best: "Habitat Lower Austral Zone freshwater marshes." Opler & Krizek offered instead (p. 242): "To date, the Rare Skipper is known only from lower brackish reaches of the Wicomico River (Maryland), Chickahominy River (Virginia), Cape Fear River (North Carolina), Santee River (South Carolina), and Savannah River (Georgia)."

Consider *Mitoura hesseli*. The species' sole larval host is Atlantic White Cedar, *Chamaecyparis thyoides*. One can see from any recent tree treatise (such as Elias, 1980, *The Complete Trees of North America*, pp. 132-133) that this cedar has large gaps in its largely eastern coastal distribution. Opler & Krizek's map for Hessel's Hairstreak shows a tracking of much, but not all, of the range of this larval foodplant, with hopscotch-like jumps in the butterfly's distribution from Virginia southward (no surprise). Opler & Krizek's map also correctly shows no records from Connecticut, something that has vexed us residents for years (a singleton was finally located in the east-central extreme of the state in 1986, by Chris Maier of the Connecticut Agricultural Experiment Station). Scott doesn't speak to the disjunctions in the cedar's range, and fills in the entire eastern seaboard for the hairstreak's home territory, from northern Florida clear up to southern Maine.

One might possibly excuse this sort of sloppy accounting if "poetic license" were being taken with all the maps (a tack of debatable utility in and of itself in anything other than a coffee-table book). However, Scott's maps for western species often sport minute zigs, zags, and holes. Thus, it wasn't a matter of the resolution capabilities of Stanford University Press' printers either...

4. Taxonomic decisions

Like Shapiro, I heartily endorse a return to conservative generic nomenclature for North American butterflies. Opler & Krizek did so for the eastern species, and now Scott blessedly finishes the task off for all the taxa. As Shapiro also notes, generic nomenclature is as much art as it is hard science; it will always remain a matter of taste.

Now, delimiting species boundaries for the great majority of our taxa has never posed much of a problem, whatever flavour of taxonomy was practiced on them over the years. North American Lepidoptera volumes treat this great majority identically (as does this new book). But these easy taxa are really only of passing alpha taxonomic interest — the volatile ones that resist initial sorting are the creatures of intrigue. Within this troublesome residuum is where one hunts for an author's taxonomic mettle.

In Part III (pp. 157-504) Scott essentially adopts the following taxonomic approach: (a) if allopatry and/or parapatry, then subspecies; (b) if (a) and/or differences slight, and/or variation not eyeballable, then synonymize. He summarily lumps the bulk of the tough Nearctic species and their subspecies — and then some, even combining several old and new world taxa — with neither justification nor deftness. As a colleague remarked to me, "it would have been more helpful to point out to the reader where taxonomic controversy lies rather than to try to hide it with sweeping proclamations lumping [many] taxa."

Shapiro offers a good rebuttal of the lumping in western *Hesperia*, and discussion of the problem of unilaterally lumping all Cupressaceae feeding *Mitoura* save *hesseli* into *gryneus* (fortunately this is an instance where Scott cross-references his foodplants to the various taxa, so that at least some of the

intriguing host-specificity issues in these hairstreaks are still extractable).

Typical of the plight of other lumped taxa are the *Chlosyne*. Scott dumps (pp. 306-308) a bevy of names into the single pan-western species *gabbii*, including, among others: *gabbii, neumoegeni, sabina, acastus, vallismortis, dorotheyi, whitneyi,* and *damoetus*. Here Scott narrowly evades embarrassment, via a footnote tucked into the bottom of page 307 at the last minute, in which he must acquiesce that at least *gabbii, acastus,* and *damoetus* need to be retained at the species level — as they always had been before him, from Emmel & Emmel (1973) through Howe (1975) to Ferris and Brown (1981).

Even with its avowed emphasis on including biological facts about butterflies, Scott's book overlooks some well-known instances of sibling species awaiting formal recognition. Consider the two virtually certain sibling *Megisto* in the northeast. Here the staccato text *is* so brief that it's wrong, as Scott (p. 237) offers: "One flight, June-E July northward." Opler & Krizek (p. 185) offer: "The Little Wood Satyr is univoltine over most of its range...the two emergences in Virginia and Pennsylvania (late and May through June and then early July to mid-August) and some other locations that follow each other so closely strongly indicate that two cryptic siblings must be involved."

Shapiro's review of the taxonomy ended by saying "Scott may be right a lot of the time." However, this begs the whole issue. Let me put it to you another way: my wife is *also* "right a lot of the time" if I ask her to sort a box of butterflies (she's a pianist, with no training in lepidopterology, but owns a keen eye and a bolt of common sense). The point, of course, is that *every one of you readers* is also "right a lot of the time." You're all expert taxonomists to a certain degree. I would never hold my wife to figuring out the tough taxa in that box of butterflies...but *you* should insist that an author of a major treatise be able to work deftly with all the taxa — not just the trivially simple ones — and show temperance, and a capacity for something other than summary execution of names.

5. What the book offers the butterfly enthusiast of the 1980s

Where has lepidopterology been during the past decade, and where is it heading? For one, Lepidoptera conservation has gone through its painful growing stage and come into its own, and is gathering more steam as time moves past. Personal and community awareness of the joys and benefits of butterflies are soaring, thanks to the path-breaking efforts of Bob Pyle and others. Butterfly photography is booming, as is butterfly watching and gardening. And natural history work, notably rearing, is taking hold again. Popular interpretive books are all the recent rage.

This represents a fundamental shift in emphasis in North American lepidopterology. We are beginning to experience what the British and others in the Palearctic have in their recent past history. What does Scott's book say to these trends of the times? Essentially nothing.

Absent from the book are segments on butterfly gardening, and scarcely a paragraph can be found on awareness, watching, and photography. Discussion of these aspects of butterflies' lives is what one might expect from a properly executed "Natural History" (witness the subtitle of this book). Opler's review torpedoed Scott's passages on Conservation and Extinctions (pp. 110-111) as "a rationalization that says collecting of rare species is all right and condones secrecy for local colonies of rare butterflies. This unbalanced discussion does not

mention endangered species efforts on behalf of insects, completely omits the Xerces Society, and fails to mention the butterfly habitat conservation accomplishments of the past ten years." I had hoped that Scott's "The Butterfly Census" (pp. 111-112) would be a discussion of the utility of butterfly counts and other relative censusing procedures, but instead I found it to contain statistics of lukewarm interest, such as guesses of the number of individual butterflies currently residing on the planet.

6. Conclusions

What do I recommend? If you already own the other books mentioned above, then I can't advise adding this one to your library. Only Parts I and II of Scott's volume have lasting value, and even so, the lack of accountable referencing palls their use as sources for science and otherwise. I *will* recommend that you think seriously about adding Opler & Krizek (1984) to your library, even if you presently live west of their covered region. They established a true standard for all of us. Future butterfly books for North America should follow their healthy lead.

7. Postscript

Stanford University Press deserves a healthy reprimand for letting such a heterogeneous volume out of the house by itself without further review. At the barest minimum, their editors should have stripped the pompous crowing from the Preface and elsewhere — and replaced those passages with appropriate modesty and circumspection, as befitting any large book in any field.

Stanford University lepidopterists have certainly sung loud songs in the 1980s about the supposed poor merit of other major works on North American butterflies (see the common names and generic nomenclature squabbles in this journal and elsewhere). I guess "what goes around comes around" — Stanford should wag its tail between its legs and beat a hasty retreat, now that the Scott book wears the name of that institution on its spine. Oh, incidentally, I happen to be an alumnus of those same Stanford butterfly laboratories, but happily cast my allegiance elsewhere in this instance.

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Like the migrating monarchs which return annually to their besieged Mexican wintering grounds, lepidopterists themselves make a similar pilgrimage to the bookstores. They return with gutted wallets to their infarcted bookshelves with *yet another butterfly book*. This obsession with acquiring books on butterflies is rivaled only by butterfly collecting itself, so aptly compared to masturbation in an article we have long since lost. That author suggested that butterfly collecting certainly feels good, but you're really not sure why. You really don't want anyone to see you doing it. But, nevertheless, when you're done, you know you're going to do it again.

We need to crowbar a space between a multivolumed "butterflies of the world" by a creationist and a couple of previous "butterflies of North America" one by a

minister and another by an artist. (Actually, we can now get rid of the latter—the one with, inexplicably, the neotropical butterflies on the cover, and Mexican butterflies for the frontpiece.) Voila, just enough space for the best book to date on North American butterflies. Refreshingly, this one is by a biologist, frankly all too rare an event. Very simply, Jim Scott knows more about his subject than anyone else alive. Scott also might euphemistically be called a free spirit. His unique opinions, which pervade this book, will amaze and enrage just about everybody.

The text is incredibly rich in detail on many aspects of natural history and butterfly biology. The larval host plant lists are truly awesome, seemingly every published record and many more are included. The introductory chapters are by far the best of their kind anywhere. All this in Scott's typically turgid prose which is scattered with the Scottisms for which he has often been criticized. Butterflies "sipping mud," indeed.

A rigorous text on North American butterflies will, by necessity, fall somewhere between research reports in professional journals and a simple guide with species descriptions. This sophisticated work, in comparison to previous treatments, leans in the former direction. The decision, therefore, to forego citations and bibliography, we think, was a mistake. Although some ideas and observations are attributed to their sources with an initial and last name, many, even most, are not. This gives the impression that a given statement is common knowledge in butterfly biology, or that the source is Scott himself—frequently neither are the case. Worse, many illustrations bear striking resemblence to ones in previous works, a debt which is generally not adequately acknowledged.

By numbering the butterfly species he includes, Scott cannot help but send the reader to Miller and Brown's 1981 checklist for comparison. Where Miller and Brown list 763 species, Scott finds just 679, a decrease of 12%. This is not due to five years of rampant extinction among the butterflies, but instead, to the most dazzling exercise in taxonomic lumping of all time. Indeed, that large drop in species is buffered by inclusions of several newly recorded southern migrant species, the recognition of several new sibling taxa, and the amalgamation of several nearctic taxa with palearctic species. Thus the decrease in species-level taxa is actually on the order of 16%, much the result of a number of truly thought provoking "new" combinations, which will have many lepidopterists doing homework.

The rationale presented for several of these new treatments is rich and solidly argued; for instance, that for one of Scott's pet groups, the *Callophrys*. For other species, such as *Euphydryas chalcedona* and *Papilio glaucus*, the lumping reflects common sense and a recognition that there is insufficient information to support specific status for many long-recognized taxa. Yet the linking of some putative species into widespread, exceedingly variable superspecies, such as *Mitoura gryneus* and *Coenonympha tullia*, will surely invite some argument.

With Scott's taxonomy and nomenclature in print (which largely supports that of Opler and Krizek's recent book) now we can finally bury the ludicrous nomenclature that brought us *"Gaides," "Hyllolycaena," "Artogeia,"* and the rest. We strongly suggest that Scott's work constitute the guiding nomenclature for all students of the North American butterflies. The fractionation of genera and blanket acceptance of poorly supported species descriptions in the checklists

of Miller and Brown and the field guides of Pyle and of Tilden and Smith can now be laid to rest.

Scott, however, has picked an unfortunate time to become extraordinarily cavalier about subspecies. Notwithstanding arguments over the "value" of subspecies and their evolutionary meaning, the subspecies is recognized by the United States Fish and Wildlife Service as the lowest invertebrate taxonomic category which can be conferred protection under the Endangered Species Act. The practice of wholesale lumping of subspecies has but one real world result — our ability to conserve those entities it compromises. To suggest, for instance, that *Euphydryas editha* consists of but three ecological and genetic segregates that are phenetically separable into subspecies is preposterous. Scott wants the range of *Euphydryas editha editha* to encompass all of California west of the Sierra Crest. But Sierra foothill populations differ from coastal populations in flight phenology (more than a month), in host choice, in oviposition behavior, and by wing markings, which differ dramatically enough that effectively every specimen can be assigned to its foothill or coast source at a glance. We are not sure what *Euphydryas editha rubincunda* means in an evolutionary context (whether or not it is a species in *statu nascendi*), but assuredly it is an entity sufficiently genetically distinct from *Euphydryas editha bayensis* to warrant subspecific recognition. Hardly a coincidence, all of the subspecies named previously by Scott himself are included, and virtually all names in his "favorite" genera are acknowledged (few of which are significantly better than of many which he has dispensed).

For most of us blindly driven butterfly book collectors, the most important feature of any work is the quality and accuracy of the figures. One of our colleagues has suggested that in Scott's book, "the illustrations suck." That is, perhaps, a bit strong. The illustrations, however, do not make for a really lovely coffee-table book. The plates are crowded, the orientation of specimens is inconsistent and many are damaged. But, having seen the original prepublication prints, the reproductions ended up surprisingly good. Arguably they are more useful for identifying specimens in hand than the figures in most other books. (Which naturally brings up the subtitle, claiming that this is a "field guide." We, for two, are having a bit of difficulty figuring out into which pocket this three pounds of "field guide" is supposed to fit!) The plate legends and figure arrangements, however, are really cumbersome. While finding the species writeups from the illustrations is simple, linking text to plate is a royal pain. It is nice however, finally, to see a butterfly book include lots of photos of living butterflies, larval stages, and eggs.

But, more difficult to follow yet are the identification keys. Instead of using traditional couplets, Scott's keys list traits with a reference number at the end of each intended to guide the reader. This make it almost impossible to enter the key at any point except at the beginning. Most enthusiasts would probably know the difference between a papilionid and a nymphalid, but separate keys for major groups of butterflies are not easily located within the cumbersome general key.

Acknowledging that by the time this review appears, all real butterfly buffs will have this book (and it probably will be remaindered, for that matter), we nonetheless toss in our nickle's worth that this will probably be *the* book on North American butterflies for a very long time. We can't imagine anyone

trying to follow, or wanting to follow, Scott in such an endeavor.

We do, however, additionally suggest that before throwing away Howe's book, that you save the color plates which, when laminated, make particularly festive placemats for those special occasions.

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A FIELD GUIDE TO WESTERN BUTTERFLIES. Tilden, J. W. and A. C. Smith, 1986. 370 pp., 48 plates (24 in color) plus text figures; Houghton Mifflin Company, Boston. Price $12.95, soft (also available in hardback).

Timing may not be everything, but the appearance of Tilden and Smith's "new" book sandwiched between the publication of the two best recent books on North American butterflies by Paul Opler and George Krizek (1984) and Jim Scott (1986) certainly will not add to its popularity. *A Field Guide to the Western Butterflies* has the standard Peterson Field Guide Series format with introductory chapters, species accounts, plates (with the familiar arrow system pointing to key identifying marks), and appendices including a checklist with "all" western butterflies and their subspecies. It covers North America west of the 100th meridian (with Alaska and Hawaii) and "partial coverage of northern Mexico."

As a western version of Alexander B. Klots' (1951) landmark *A Field Guide of the Butterflies of North America, East of the Great Plains*, this book has been long overdue, and should fill a glaring gap in the Peterson series. But, Tilden and Smith's book apparently has been in the works for well over a decade and unfortunately it shows...over and over again. The last decade has seen an explosion of information on the biology of butterflies. That explosion has been fed by an immense increase in knowledge of the distributions and evolutionary relationships of our butterflies. A number of state and regional monographs (Emmel and Emmel 1973, Dornfeld 1980, Ferris and Brown 1981) and a variety of checklists and research papers on the western butterflies make these insects a very well known group in a well studied region. In this light, Tilden and Smith's work is something of a relict; the amount of quite readily available information lacking is really shocking.

Considering all the recent attention paid to North American butterfly taxonomy, we cannot be more disappointed that one more book is using an unacceptable nomenclature. This situation is not only unnecessary, but is particularly ill-advised in a guide for lay persons. There is virtually no explanation of the origins of Tilden and Smith's taxonomic treatment except on page 1 where they stated that they followed Klots' sequence of families. Not so. Klots recognized 11 families and followed Nymphalidae with Libytheidae whereas Tilden and Smith inexplicably discuss 12 families and place the libytheids between the Pieridae and Riodinidae. The order of families used is hardly most important but it succeeds in thoroughly obscuring relationships among butterflies as we know them. The recognition of 12 families of butterflies itself is totally unsupported. The evidence is abundant that butterflies belong at most to 5 or perhaps 6 families (Ehrlich 1958, Ackery 1984, Scott 1984).

The nomenclature appears to follow Miller and Brown (1983). Yet as Opler and Krizek's and Scott's recent books indicate, responsible workers continue to use a much more conservative nomenclature. Tilden and Smith have never met a taxon they didn't like at any taxonomic level. They include the widely discounted genera *"Occidryas"*, *"Artogeia"*, *"Hyllolycaena"*, and *"Falcapica"*. Their presentation of the *Euphydryas* is typical. That generic name cannot be found except with a notation stating that the name was *"replaced"* in 1978. Higgins (1978) provided no evidence whatsoever for his generic demolition. Nonetheless, ignored from the same year was the much more careful work of Scott (1978) suggesting that *Euphydryas anicia, E. chalcedona*, and *E. colon* form a *rassenkreis* and hence constitute a single species.

If the *Euphydryas* species are confusing in this book, the presentation of *Euphydryas* below the species level is positively stultifying. No fewer than 21 subspecies of *E. editha* and of *E. "anicia"* are listed in the "checklist/life list." Yet only three of each are illustrated and discussed in the text. Those three account for but a percent or so of the overall distribution of either species. In contrast, all nine checklist subspecies of *E. "chalcedona"* are presented in the text, but only two are illustrated. How, for instance, *E. c. kingstonensis* ("salmon-colored, dark markings small") is to be distinguished from neighboring *E. c. corralensis* ("spots light red, dark markings narrow") is not clear. The lay person who could identify a checkerspot to subspecies has to be using another book.

Unfair example? We don't think so. In the western states, rimmed and divided by young mountain ranges, confounding species groups are hardly the exception. *Euphilotes, Chlosyne, Speyeria, Phyciodes, Pontia, Euchloe, Erynnis, Thorybes, Hesperia*, and the *"machaon"* swallowtails are but a few of the troublesome groups containing hundreds of taxa. For these and other genera and species groups, this book will confuse rather than guide in the field.

The treatment of subspecies in general is terribly uneven. Granted, some were described too late to be included. But where is *Plebejus shasta charlestonensis* (Austin 1980)? Scott (1981a) named 18 new subspecies, but only 7 of these are included. Most (or all) the other eleven represent very distinct phenotypes but are omitted for some unknown reason. For some species all recognized subspecies are mentioned in the species accounts, their distributions given and they are briefly characterized. For others, there is no mention except that there are some similar subspecies. Still others are grouped as sets of similar phenotypes.

Arguments for and against the use of common names have been well aired but one thing on which all agree is that for common names to be useful, they must be standardized (Murphy and Ehrlich 1983a, Pyle 1984, Austin 1985a). This book certainly is not a step in that direction. Tilden and Smith present 41 species of satyrines corresponding to those in Pyle (1981) but only 23 of these share the same common names. Considering the principally lay audience of this book, this lack of nomenclatural concordance is hardly trivial. Tilden and Smith go on to give each subspecies a common name as well. Suffice to say that even the bird people did away with that attempt long ago.

Not surprisingly, these points alone add up to an immensely confusing field guide, which fails at the most fundamental level for a field guide, it does not facilitate the association of names with organisms in hand. For example, the guide is useless in the field for separating any of the *Euphydryas* species (less the extremely distinct *E. gillettii*). As Murphy and Ehrlich (1983b) pointed out, *Euphydryas editha* usually may be distinguished from members of the *E. chalcedona* complex by an easy diagnostic feature — the former lack white spots

on the dorsal portions of the plural region of the abdomen. That simple "in hand" character solves the confusion nearly everywhere where species overlap in the west.

Then again, perhaps, we should give Tilden and Smith the same break we might give *A Field Guide to the Stars* or *A Field Guide to the Animal Tracks*. Actually, many of our complaints with their book center on subspecies level information, and no other contribution in this series attempts to do so much at that level of taxonomic resolution. *A Field Guide to the Western Birds*, for instance, dabbles merely with the very well differentiated subspecies. But, while that does limit the information content, the information included is largely correct.

A Field Guide to the Western Butterflies, by comparison is a veritable cacophony of errors when it comes to the distributions of butterflies. Many of the errors simply repeat old ones, which suggests that the authors have not kept up with the literature. Taking, for example, an area with which both of us are familiar — the state of Nevada — you'll get an idea of the extent of the distributional disinformation. Although Austin and Austin (1980) is listed in the bibliography, a substantial proportion of their distributional records are not included. Other information is somewhat newer but certainly was available (*e.g.,* Ferris and Brown 1981, season summaries of the Lepidopterists' Society, *etc.*). Anyway, despite what Tilden and Smith say, *Cyllopsis pertepida, Calephelis wrighti, Ministrymon leda, Callophrys comstocki, Euphilotes battoides martini, E. enoptes dammersi,* and *Systasea zampa* are all resident in southern Nevada and *Coenonympha california, Anthanassa texana, Phyciodes phaon, Heliopetes domicella,* and *Chiomara asychis* all stray to southern Nevada. *Basilarchia archippus lahontani* is restricted to northern Nevada; those elsewhere are a different phenotype. The hybrid *B. weidemeyerii latifascia X B. lorquini lorquini* occurs at several locations in western Nevada. *Speyeria egleis toiyabe* occurs in central Nevada and not north-central Nevada. *Anthocharis cethura* is not in central Nevada but in southern and western Nevada (*A. pima* synonymous). *Polydryas arachne* occurs in southeastern Nevada. *Hypaurotis crysalus* is known from eastern Nevada. *Callophrys affinis* occurs to central Nevada. *Incisalia fotis* occurs in parts of western Nevada. *Lycaena nivalis* near *browni* occurs in northeastern Nevada. *Plebejus lupini* occurs east at least as far as eastern Nevada. *Euphilotes enoptes ancilla* is more than Rocky Mountain in distribution, occuring through much of northern Nevada (see also Shields 1977a). *E. rita pallescens* is not in southern Nevada but in central Nevada (see also Shields 1977b). *E. spaldingi* is in eastern Nevada. *Megathymus coloradensis* is only in southern Nevada. *Euphyes "ruricola"* (= *E. vestris*) is on the east slope of the Sierra Nevada in extreme western Nevada. *Hesperia lindseyi* is in northwestern Nevada. *Pseudocopaeodes eunus* occurs also in central and western Nevada. *Erynnis propertius* is in extreme western Nevada (all Austin 1985b). *Cercyonis pegala blanca* is a synonym of *C. p. stephensi* and the latter is not a form of *C. p. ariane* — *C. p. ariane* does not occur in Nevada. *Polygonia hylas* is a subspecies of *P. faunus.* (Ferris and Brown 1981). *Speyeria zerene pfoutsi* is a synonym of *S. z. platina* (see Grey and Moeck 1962). The *Speyeria mormonia mormonia* phenotype is not found in Utah and *S. m. arge* is a synonym. *Charidryas palla vallismortis* is not a *C. palla* subspecies but closer to *C. acastus* (*fide* J. F. Emmel). *Thessalia leanira cerrita* is a synonym of *T. l. wrighti* (the types were both from virtually the same place) and the Mojave Desert popula-

tions presented as *"cerrita"* are unnamed. The type locality of *Neophasia menapia* is not in Utah, but probably in western Nevada since Pierre Lorquin was never in Utah (see Miller and Brown 1981, Scott 1981a). *Apodemia palmerii palmerii* and *A. p. marginalis* are synonymous. *Calephelis nemesis dammersi* is the summer form of *C. n. californica*. The form "ines" of *Ministrymon leda* also occurs in the early spring. *Satyrium dryope* does not occur in Mono County, California; what is there is a large, pale, and sometimes tailless *S. sylvinus*. *Plebejus icarioides ardea* is a synonym (actually an aberration) of *P. i. fulla*. *Hesperia pahaska* occurs in S. Nev. not "S. Neb." A number of taxa are attributed to the Nevada fauna which apparently have no basis in fact: *Oeneis nevadensis*, *Lycaena x. xanthoides*, *L. mariposa* and *Poanes taxiles*. And, it is certainly a lapse to separate *Anthocharis* and *Euchloe* from *Pieris* (s.l.) by the Coliadinae. *Anthocharis* and *Euchloe* belong together with other whites in a single subfamily, the Pierinae, distinct from the Coliadinae (Geiger 1980).

These are problems culled on a quick glance from the standpoint of just one state!

We have not checked all the hostplants listed but spot checking some of those identified as mistakes by Scott (1981b) shows that many are again repeated incorrectly. More obvious, and important, to a field guide are the mistakes in habitat associations. *Speyeria egleis*, in Nevada, is a hilltopper and an edge species, occurring along shaded roads and openings. *Speyeria mormonia* is montane occurring mostly in wet meadows. *Phyciodes orseis herlani* does not occur in "mountain meadows"; it is found along wood edges and in forest openings. *Chlosyne neumoegeni* uncommonly occurs in desert scrub, but nearly always along washes. *Chlosyne lacinia* is common in agricultural areas. *Phoebis sennae* is a desert species in parts of its western range. Great Basin *Anthocharis sara* are mainly found in the pinyon-juniper woodlands. *Callophrys lemberti* also occurs along washes and hillsides at relatively low elevations in the Great Basin. *Polites sabuleti tecumseh* occurs in upper montane and subalpine meadows and is not restricted to the alpine. And, what is meant by *"Occidryas"* (these are all *Euphydryas*, Brussard *et al.* 1985) *chalcedona* being "a dominant in its range"? The statement certainly has no biological meaning.

And the illustrations, do they really measure up to the standards of a good field guide? Tilden and Smith might get a gentlemen's "C" on that front. Most of the black and white plates are clear, although some such as Plate 25 are a little fuzzy. The outlines of many of the more pale butterflies were darkened to make them stand out against a white background. This looks unnatural and easily could have been cured with a darker background. Some, such as Plate 44, look a little dark overall. The Peterson Field Guide Series, as a whole, generally has excellent color but this one suffers. Several (such as Plates 9, 12, 14) are far too yellow. Plate 21 is far too pale, the lycaenid plates are either too dark or are off color. Plate 13 figure 2 looks to be a *Speyeria coronis* rather than *S. zerene* and *S. callippe nevedensis* is much greener than figure 6. Plate 14 figure 4 is a pale *S. mormonia eurynome* (*S. m. mormonia* is not in Utah). All the plates lack the crispness of the plates in other field guides of this series.

For our money, we'll take Bob Pyle's field guide in the Audubon series, or the Ehrlichs' (1961) classic. Neither tried to do as much; both did what they did well. And, we will continue to look forward to Opler giving us a "West of the Great Plains" as good as the "East of the Great Plains". It won't fit in our pockets, but at least we'll wish it did.

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BUTTERFLIES OF THE HIMALAYA. Mani, M. S. 1986. 181 pp. Dr. W. Junk, publisher, Dordrecht. Price: $79.50.

Victims of crime often speak of feeling "violated." To buy this book is to invite that feeling. The price, $79.50, is *not* a misprint. It comes out to 44¢/page, which is about what the most expensive technical monographs run nowadays. Professionals — scientists, scholars, physicians and the like — have gotten used to paying such prices. Publishers justify them on the ground that technical monographs have small audiences and small press runs and are thus very expensive to produce. The prices are softened a bit by our ability to write such expenses off on our income tax returns as "professional expenses," and the availability of grant money to buy publications needed for research. Even as prices skyrocketed in the past decade, the esthetics of technical books deteriorated. To save money, fewer and fewer such books are actually set in type. More and more, they are printed by photo-offset from typescript ("camera-ready copy"); they thus look like legal briefs between covers and are ugly and jarring to the eyes of those who truly love books. We have gotten used to that, too, in the same sense as one of my math teachers once informed the class (referring to homework) that "you can get used to hanging if you do it long enough."

Butterflies of the Himalaya is set in type, and that is about the only good thing one can say about it. Because it actually looks like a book, one is unprepared for what lies beyond the title page. There are many words to describe this book, and most of them are unprintable.

There is no evidence that the manuscript was ever copy-edited or the proofs checked for typos — at least not by anyone who reads English. In a haphazard sample of ten pages I found over 5 typos per page (many of them both egregious and obvious) and 2 grammatical errors, usually involving omissions of particles or the like. The impression of slovenliness is further compounded when one gets to the illustrations.

There are a few color photos of habitats, reduced to the size of a block of four postage stamps and virtually useless. Anyone who wants a visual impression of

the Himalaya would do much better with a backfile of *National Geographic*. The captions are confusing at best. The term "steppe" is used there and in the text for what we would call "woodland," as in California foothill woodland. The photo of the "abode of high-altitude butterflies" shows a snowfield. The "high-altitude meadow with *Thermopsis* in bloom, the home of *Colias* butterflies," is a close-up of *Thermopsis* in flower. There is a picture of "*Papilio* butterflies congregated in swarms." There is no explanation of why they are congregated in swarms. Maybe they really are Danaid-mimicking *Graphium* (not *Papilio*; Mani himself uses *Graphium*), but they look like Danaids to me and are acting like them, too.

After this the illustrations deteriorate rapidly. Many of the specimens figured are abominably set. None has any data given. Even the sexes are not specified. The *Parnassius* are shown in color, photographed against a distracting sky-blue background full of vague shadows. The black and white illustrations defy description. There are four photos to a page, arranged in a rectangle 2 × 2 starting at the bottom of the page. They are to different (unspecified) scales; some are out of focus; and — unbelievably — some are cut off at the edges, like the headless snapshots of Uncle Harry at the family reunion. But the best is yet to come: the caption-identifications are very nearly random *vis-a-vis* the animals illustrated. Sometimes the names are in the wrong positions; sometimes they refer to photos on different plates; and sometimes they refer to species not illustrated at all. Consider the Pieridae. On plate XIV, "*Pontia daplidice*" is actually a *Euchloe*; the real *daplidice* appears on the same plate as *P. glauconome*; on plate XV "*Pieris dubernardi*" is actually *Pontia callidice kalora*, and "*Pontia callidice*" is an *Appias*; on plate XVI "*Euchloe ausonia*" is a *Pieris*... and so it goes.

The taxonomy in the text is nearly random, too. On p. 34 under the heading "Zerynthidae" (note family ending), the first sentence begins "The butterflies of this subfamily are recognised..." and the paragraph concludes a few lines later with: "This was formerly considered a subfamily of Papilionidae." I will not try to correct all the equally absurd errors, but to give the flavor of this magisterial work, I note that *Argynnis* (p. 121) includes *Brenthis; Limenitis* is consistently misspelled *Liminitis; Vanessa* (pp. 118-120) incorporates *Vanessa sens. str.* as well as *Nymphalis, Inachis*, and *Polygonia* (!)...and so it goes.

The distribution maps show no physiographic features — just a schoolboy's outline map of the Indian subcontinent and Southeast Asia with a handful of symbols; the lettering is childish and the symbols are indistinctly drawn freehand. Rarely have so many uncircular dots appeared together in public.

The Hesperiidae are not included.

I bought this book because the publisher's advertisement promised a concluding synthesis of biogeography. Its principal point — that the Himalaya has a remarkably unbalanced, undiverse, immature fauna with nearly all the endemism confined to the alpine zone — could have been made in a five-page paper, *and should have been*.

Mani did us all a great favor 25 years ago by publishing his *Introduction to High-Altitude Entomology*. My copy, now worn and tired, literally guided me into the high-altitude research I now do in the Andes, though as I got further and further into my work I realized more and more that much in Mani's book is inadequately documented and even dead wrong. Still, I know he knows his Himalaya, and I deeply regretted his failure to attend and present his scheduled paper at the Latin American Congress of Zoology in Arequipa. I thought this

book would substitute. But this book is a disgrace to Mani and to the publisher. It should never have appeared in book form at all; it could easily have been published as a long faunistic paper in any of several respectable British or Indian journals, in which form it could have reached its proper clientele at sensible cost and under better editorial control. Once a decision was made, however, to publish it as a book the publisher had an obligation to assure quality at all levels, and this he failed to meet. The book was actually set and printed by IBH Publishing in New Delhi, but it bears Junk's imprint and Junk is responsible for it. Junk used to be a very respectable, if always pricey, publisher of important technical monographs. Now, apparently, it is living up to its name. It is still pricey, but it now publishes *junk*.

Anyone who buys this book is an accomplice to his own victimization. As a professional, I can write it off on my tax return — but I am almost ashamed to admit I bought the damned thing.

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BREEDING OF BUTTERFLIES AND MOTHS
Ekkehard Friedrich, 1986. Translated from German by S. Whitebread, supplemented and edited by A. M. Emmet. 176 pp., 46 figs.; Harley Books, Colchester (Great Britain). ISBN 0 946589 20 8. Price £5.95 (hardback).

Friedrich's "Handbuch der Schmetterlingszucht" (2nd edition 1983) has become a "classic" for all breeders of butterflies and moths in German speaking countries. The present first English edition is rather late on the market. The book consists of two distinct parts. In the first part ("Basic principles") the methodological description of breeding of butterflies and moths is provided; it includes topics as breeding equipment and techniques, hand pairing, cages, storage of eggs and pupae, hibernation, transport, conservation, artificial and semisynthetic diets (the last topic rewritten by B. O. C. Gardiner) etc. The second part of the book ("Rearing descriptions") gives detailed descriptions of breeding many European Lepidoptera, species by species, divided into three subsections: butterflies, "larger" moths and "micro" moths (the last subsection written by A. M. Emmet). The book closes with a useful select bibliography, information on entomological societies, addresses of specialist booksellers, suppliers of equipment and seedmen. The first part of the book under review is well illustrated, but lacks information on some modern techniques and equipment (e.g incubators are now common in most laboratories and surely not out of reach of many amateur lepidopterists: they enable the breeder to maintain the desired temperature and humidity, the better models can maintain the desired photoperiod and different night and day temperatures). Since the book contains instructions on how to kill adult butterflies and moths, I would have expected to find instructions on how to preserve early stages, particularly the caterpillars, utilizing modern methods (e.g. freeze drying). All in all: Friedrich's book is a most welcome addition to lepidopterological literature in English language; it will surely and deservedly become a best seller. Compared with the German edition, it is much better produced (printing, quality of paper, contents) and the

superior English hardback sells for less than a half of the price of the inferior
German paperback.

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WIESEN UND BRACHLAND ALS LEBENSRAUM FÜR SCHMETTERLINGE.
(in German; English summary) Erhardt, Andreas. 1985. Birkhäuser Verlag,
Basel, Boston, & Stuttgart. 154 pp., 2 color plates, 89 text-figs. sFr. 69.

The socioeconomic context of European agriculture is changing. Pastoral
methods established in the Alps over many centuries are being supplanted by
intensive fertilizing and mowing of the better pastures, and abandonment of
the poorer ones. Because so much of the diurnal Lepidopteran fauna of the
region is associated specifically with montane and subalpine meadows man-
aged in the traditional ways, Andreas Erhardt undertook to examine the
impact of the new methods on that fauna. His results are alarming. They are
presented here in a magnificently-produced monograph which is a sophisti-
cated ecological study, though superficially packaged as a coffee-table book.

Using adaptations of European phytosociological techniques (generally un-
familiar to Americans, and coolly received by most plant ecologists this side of
the Atlantic), Erhardt characterizes the vegetation of traditional and modern
pastures and its correlation with Lepidopteran fauna. He finds that both
intensified fertilization and cutting cycles and abandonment are catastrophic
for many species, including some of special concern. Indeed, entire species may
be lost from the Alps if protective measures are not taken. Ironically, "protec-
tive measures" in this case means setting aside some carefully selected pas-
tures and managing them as they have been managed since Wilhelm Tell's
day.

How is it possible that *native* butterflies and moths could owe their continued
existence to the maintenance of grazing *disclimaxes*? Lepidoptera are, by and
large, not animals of climax forest. The common notions of "balance of nature"
and "pristine communities" are also exceedingly naive. Throughout the Qu-
aternary (Pleistocene and Holocene=Recent), climate has fluctuated and with
it, plant and animal communities. Human impacts provide an additional layer
of disturbance, but that disturbance benefits some organisms as it damages
others. Thus, many meadow butterflies and moths of the Northern Hemisphere
are ill-adapted to the climax forest biomes currently dominant there. They
represent relics of the drier steppe-tundra conditions around the continental
glaciers, and have kept going only through natural and man-induced deforesta-
tion which produced local "mini-steppes" for them. The most stable of these
have probably been the grazing disclimaxes of Erhardt's montane meadows,
and it should not be all that surprising to find them supporting rich and
specialized faunas. The British learned too late that grazing was prerequisite
for the persistence of their Large Blue, another beast at the edge of its climatic
tolerance. In that case, grazing acted by producing conditions favorable to the
ant species on which the Blue was dependent. A glimpse at the distributions of
the genus *Maculinea* quickly underscores how marginal *M. arion* was in
Britain. The same is true of many Alpine meadow species. Ironically, the
massive tree die-off in central Europe (which seems to be a synergistic effect of

pollution and climatic change) may yet come to their rescue.

Erhardt's study must not be generalized glibly. In northern Europe a higher percentage of species appears well-adapted to brush- or heathland, so abandonment of pasture could be a more favorable development there. In North America we know almost nothing of these matters. In the West, fire suppression has reduced the extent of successional habitat and increased that of mature forest. It has also reduced runoff and hence adversely impacted natural wetlands. One would predict a generally negative effect on butterflies, which might be mitigated by logging and moderate grazing. On the other hand, intensive grazing would be expected to have devastating effects in arid and semiarid climates and in fragile alpine or subalpine meadows with peaty soils. Erhardt's study serves as a model of what *can* be done. Ultimately, it may help us understand the global determinants of ecological diversity; presently, it points the way to local investigations and prudent assessment of risk. It should be read widely by ecologists, conservationists, and managers.

Unfortunately, the proverbial incompetence of Americans in foreign languages will impede its full impact being realized here. There is a concise one-page summary in English (p. 143) which is sufficiently tantalizing to get the timid reader of German reaching for his dictionary. There is also what amounts to a somewhat longer abstract published as an article in the English literature (Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *J. Appl. Ecol. 22:* 849–861).

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THE MACHINERY OF NATURE. The Living World Around Us - and How It Works. Paul R. Ehrlich. Simon and Schuster, New York, 320 pp. $18.95.

If your book budget for the year is $20.00, I suggest you spring for this tour de force of exceptionally clearly written contemporary ecology. I was so taken with the work that I read it through with complete attention in two sittings. Since Ehrlich is probably our most prominent lepidopterist, the book is filled with examples from his and his colleagues work with butterflies, in particular *Euphydryas editha*. Ehrlich, no slouch as a popular science writer, here gives us his most highly readible work to date. He generously ascribes a part of his writing success to the input of many peers to whom he offers his work for criticism prior to publication. I make this point to emphasize the value of having ones work read and commented on by others.

Development of the book follows what would be a logical sequence in constructing a course in general ecology, from the specific to the general, with lots of exciting side trips. The flavor of the whole comes in the introduction, subtitled "butterflies, ecosystems, and people," wherein Ehrlich starts with a checkerspot anecdote, goes on to state that nothing is more important today than understanding how nature works, and concludes that a quasi religious movement to alter popular awareness of nature may be our only hope in saving civilization.

The first chapter deals with physiological ecology, the adaptive relationship of individuals to their environment. Citing many of the exquisite attributes which

deliver the miracle of survival he goes on to the question of why. Chapter two starts with a butterfly story, the checker spot classic of Jasper Ridge, generalized to an understanding of the forces regulating numbers in a population. Anyone with the slightest real interest in Lepidoptera should know this as litany. The text is all this while threading us through evolutionary theory and its most recent arguments. Behavioral ecology, subtitled sex and society follows. Community ecology is discussed in chapters entitled "Who lives where and why" and "Who lives together and how." Life support systems is last, with a concluding essay as epilogue. The message is that natural ecosystems are rapidly being destroyed and that we still know precious little about their detail of operation. Ehrlich makes a call to action for public support and efforts of all informed citizens to educate. We must all work together to amplify this call while there is some bit of nature left.

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TAGFALTER 1. H.-J. Weidemann. 1986. Neumann-Neudamm Verlag, Melsungen (Germany). 288 pp., coll. ill.; ISBN 3-7888-0500-5. DM 38,— hardback. (In German).

This small, richly illustrated pocket book is the first of two volumes intended to present the natural history of German butterflies (the Alps excluded). The first volume deals with families Papilionidae, Pieridae and the first part of Lycaenidae. It consist of a general part dealing with butterfly ecology and a systematic part featuring individual German and contrary to the authors introduction, many non-German species. Of particular value are colour photographs of early stages (mostly taken in captivity, some are marked in this respect) and the fact that the author lists only those foodplants which were accepted by larvae kept in captivity. Most interesting is the authors original attempt to relate German butterfly species to certain phytoecological units. The descriptions of most species and their early stages are very poor; time and time again the author tells us just that the caterpillar looks like a typical Lycaenide larva. This is as useful as D'Abrera's infamous statement "♂ as illustrated". Much information has been taken from other publications, without any reference to the source of information. Thus Weidemann deals with the K- and r-strategy in butterflies using a formula from a German ecology textbook and the ecological properties of species exhibitions either K- or r-strategy are taken from an English textbook. The species are classified by the formula without ever obtaining the data (i.e. populations sizes) of the species concerned. Further, this distinction is in connect as all butterflies are r selected (see Pianka, E.R. 1970. Amer. Nat. 104:592-597). The attempt to present information on population ecology of German butterflies is a change for the good, as such information, in contrast to British Butterflies, is almost non-existant. For a country where widespread extirpations have already occurred the situation is deeply troubling. The book pays more attention to butterfly life histories than any standard German publication. It does not reach the standard of the much larger Swiss publication "Tagfalter und ihre Lebensräume" reviewed in this journal, nor of a similar English pocketbook "RSNC Guide to the butterflies of the British Isles" by J. A. Thomas.

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